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V. *On the Structure and Development of the Skull in Sharks and Skates.*

By W. K. Parker, *F.R.S.*

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[Plates XXXIV.–XLII.]

Introductory Remarks.

THROUGH the kindness of my friends Henry Lee, Esq., F.L.S., and F. M. Balfour, Esq., B A., I am able to give illustrations and descriptions of this type of skull in a degree of detail beyond what I had ever hoped to accomplish.

Embryos and well-grown individuals of Dog-fish and Skates have been liberally supplied me by Mr. Henry Lee; these have been from the Brighton Aquarium; the embryos of *Pristiurus* and of *Scyllium*, kindly given to me by Mr. Balfour, were obtained from the Aquarium at Naples.

As the youngest of these long, delicate, vermiform larvæ were not more than two thirds of an inch in length, the *head* forming a small knob, as it were, to a long and highly flexible staff, it may be imagined how minute these objects were for operating upon by dissecting-instruments.

By zeal and patience the task has been mastered; these small heads have been made to disclose most important morphological secrets. If any biologist lives who is ready to deride this minute work, I would ask him to close his eyes to what is here shown him, and then give a full explanation of what is presented to him in the skull of an adult Skate or Shark.

As the Osseous Fishes have undergone a large amount of metamorphosis or specialization, as compared with these Selachians, more than is seen in the Ganoids, it seems natural that the Selachians should stand in a low place, zoologically. This, in many respects, would be, for them, a false position; for, embryonic as they are, in certain respects, in their adult state, yet they are, on the whole, a very high kind of Fish. They are sharply separated from all fishes, except the Marsipobranchii, by the non-related condition of their exo- and endoskeleton. Even in the Ganoids the exoskeletal scutes are brought under the influence of the endoskeleton in the head; and this inner framework draws, as it were, any and every convenient dermosteal patch into harmony with itself, enshielding itself with the enamelled pieces, which take on an outline that makes them apt for any such defensive service.

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It would seem therefore that where this morphological affinity has not exerted its force, the study of the uncombined endoskeleton would be an easy task. This is not the case; for there is another simple and peculiar character about the Selachian skeleton and skull, namely the absence of the ossified territories found in the cartilage; thus Nature has removed her usual landmarks. There is a calcareous deposit; but it is generally distributed over the cartilage as tessellated "superficial endostosis," a mere *calcification* of regular groups of cells, these groups having no more morphological meaning than the "placoid" grains that form the *shagreen* in which the fish is enclothed.

In researches so manifestly difficult and slow as this it is well to do one thing only at a time, and that in one part mainly. It would be out of place here to enter into a discussion as to the general anatomy of the Selachians: what follows will show the value (or the writer is much mistaken) of the study of their cranial morphology.

The present contribution to this part of biological science is, if the whole vertebrate series be considered, just simply the spelling-out of a word or two that may help, with the addition of many such essays and spellings, towards a true reading and interpretation of the skull, and of its relation to the rest of the skeleton.

But the great Selachian group may well have much labour spent upon it for its own sake; and an attempt is here made to unite and knit into one whole the labour of the gradationalist on one hand, and of the embryologist on the other.

The works whose titles now follow are for the most part gradational. The labours of the embryologist are quoted also; but those at hand are by one young and talented worker, Mr. Balfour.

The works and papers that have been of most value to me as containing descriptions of adult skulls of Ichthyopsida are the following, namely:—

JOH. MÜLLER. "Vergleichende Anatomie der Myxinoiden, oder Cyclostomen, mit durchbohrtem Gaumen. Erster Theil. Osteologie und Myologie." Abh. Berl. Akad. 1835, p. 65; Wiegm. Arch. 1836, ii. p. 245.

T. H. HUXLEY—

1. Elem. Comp. Anat. 1864, pp. 162–218.
2. "On the Representatives of the Malleus and Incus of the Mammalia in the other Vertebrates." Proc. Zool. Soc. May 27, 1869.
3. "On the Structure of the Skull and of the Heart of *Menobranchus lateralis*." Proc. Zool. Soc. March 17, 1874.
4. "Contributions to Morphology.—Ichthyopsida. No. 1. On *Ceratodus forsteri*, with Observations on the Classification of Fishes." Proc. Zool. Soc. Jan. 4, 1876.
5. "On the Nature of the Cranio-facial Apparatus of *Petromyzon*." Journ. Anat. & Phys. vol. x. pp. 412–429, pl. 17, 18.

RAMSAY H. TRAQUAIR. "On the Cranial Osteology of *Polypterus*." Journ. Anat. & Phys. vol. v. pp. 167–183, pl. 6.

ALBERT GÜNTHER. "Description of the *Ceratodus*, a Genus of Ganoid Fishes recently discovered in Rivers of Queensland, Australia." Phil. Trans. 1871, part ii. pp. 511–571, pl. 30–42.

CARL GEGENBAUR. 'Untersuchungen zur Vergleichenden Anatomie der Wirbelthiere' (part 3. Selachians). Leipzig, 1872.

Then follow in natural order, the writer's own papers in the 'Philosophical Transactions' on the structure and development of the skull in various types. The present paper is one of the same kind, but especially intermediate between M. Gegenbaur's splendid work and the invaluable researches now to be noticed.

F. M. BALFOUR—

1. "A Preliminary Account of the Development of the Elasmobranch Fishes." Quart. Journ. of Micr. Sc. Oct. 1874.
2. "The Development of Elasmobranch Fishes." Journ. of Anat. & Phys. vol. x. pp. 517–570, pl. 21–26.
3. "The Development of Elasmobranch Fishes." Ibid. pp. 677–688, pl. 29.
4. 'A Comparison of the Early Stages in the Development of Vertebrates: Studies from the Physiological Laboratory in the University of Cambridge.' Part ii. 1876, pp. 1–20, pl. 1.

Although out of order, I must mention two important papers recently sent me by the author.

BURT G. WILDER.

1. "Notes on the North-American Ganoids *Amia, Lepidosteus, Acipenser,* and *Polyodon.*" Proc. Am. Assoc. for Adv. of Sc.: Detroit Meeting, Aug. 1875. Salem, Mass., 1876, pp. 151–194, pl. 1–3.
2. "Note on the Development and Homologies of the Anterior Brain-mass of Sharks and Skates." Am. Journ. of Sc. & Arts, vol. xii. Aug. 1876[1].

I mention these last papers because of the necessity of studying the nervous and skeletal systems together, and also because of the intimate relation of the Selachians with the Ganoids.

In the following description allusion will be made to the condition of the stages of the skull in other types, especially in the Ichthyopsida.

But the intimate relation of the skull of the Amphibia with that of the Selachians is best seen in the outlying forms of the latter group, namely *Cestracion*, *Notidanus* (*Heptanchus*, and *Hexanchus*), as these come nearest to the Chimæroids on one hand, and to the larval Batrachia and Urodela on the other.

Professor Huxley's paper on *Menobranchus*, a Perennibranchiate Urodele, has been of the utmost service to me; and by the time the present communication is published, I hope to have also in print my second paper on the Batrachian skull, and my first on that of the Urodeles. These, in addition to remarks on the growth and changes of the

[1] Several fresh papers by my friends Balfour and Wilder have reached me since the above list was written.

skull in the Common Frog[1], will show what is seen in *Bufo vulgaris*, *Dactylethra capensis*, *Pipa monstrosa*, *Siredon* (with *Amblystoma*), *Seironota*, and the adult skull of the lowest Amphibian, namely that of *Proteus anguinus*.

The reader, if he compare this with my former papers on the same subject, will find that my views as to the morphological interpretation of the parts are not fixed, but oscillate, tentatively.

I hold that this vacillation is safest at present; in each succeeding paper I express the views that seem to me to be true at the time; and I would rather waver in doubt—working upwards towards the light—than become fixed in the belief of some favourite view that might turn out to be a mere verisimilitude, and essentially erroneous.

No man at present is able to say whether *all* or *part*, or, if part, how much of the "trabeculæ cranii" are ventral, or belong to the visceral-arch series.

It was not known until lately whether there were any true visceral arches between the great mandibular arch and the "horns" of the trabeculæ in the frontal wall of the face.

The interpretation of the cranial nerves is extremely difficult when it is sought to arrange them as the serial homologues of the spinal nerves—and this not merely in the nerves of special sense, but also in the common motor and sensory nerves, such as the "trigeminal," "facial," &c.

My own opinion *was* that the *facial* part only of the trabeculæ belonged to the visceral series—its terminal arch; *then* I yielded to Professor Huxley's view of the visceral nature of the rods throughout; *now* I sway back again, and think that their *subcranial* part is axial in nature.

Also as to the relation of the "visceral" to the "costal" arches, here is another heavy difficulty: in morphological "habit" they are diverse exceedingly; and whilst the latter are developed in a continuous "somatopleure," the former are solidifications of the cloven oro-faucial wall.

On the Development of the Skull and Face in the Lesser Spotted Dog-fish (*Scyllium canicula*).

First Stage: *Embryo of Dog-fish*, 8 *lines to* 11 *lines in length*.

Keeping the development of the Frog's skull in view, it may be remarked that, on the whole, the youngest embryo of the Dog-fish (Pl. XXXIV. fig. 1) is intermediate between the first and second stages described in the Frog ("Frog's Skull," pls. 3 & 4); and with these they may be compared.

The "mesocephalic flexure" was complete, the middle vesicle (C^2) projecting forwards, and the anterior vesicle (C^1) loking downwards. Everywhere very translucent,

[1] "Batrachia," Part 2, is now in print. See Phil. Trans. 1876, part 2, pp. 601–669, plates 54–62.

the skin was of extreme thinness, and composed of very delicate cells, over the greater part of the *long* posterior vesicle (C^3).

Each sense-capsule was seen, externally, to be formed by an infolding of the skin of the embryo, the "epiblast" and adjacent layer of "mesoblast."

Behind the great gaping oral opening there were six clefts, equidistant from each other, and not meeting below. This embryo, being treated with carmine, and examined in glycerine as a transparent object, showed well the cartilaginous pith inside the thick ridges that intervene between the clefts. The surface of these ridges had budded into a series of rounded papillæ, as in the unhatched Tadpole ("Frog's Skull," pl. 3, figs. 2 & 3, *br* 1 & 2); these were the beginnings of the *external gills*; they were found on all the "postoral" arches except the last. In the Frog-embryo they were not present on the first and second postorals. The object (fig. 1) has been drawn obliquely, exactly as it appeared to the eye under the microscope; the other figure (2) shows the exact *lateral* view of the parts. All but the first two postoral ridges turn directly inwards (fig. 6); the enclosed pith is a stout sigmoid rod of *young* hyaline cartilage. Such a pith exists in the first two postorals (*mn*, *hy*); but they send forwards from their point of attachment a large *pedate* process; they are subbifurcate above. This anterior fork, in the case of the second postoral, or hyoid arch, applies itself along the side of the auditory capsule. The first postoral, or rudimentary mandible, is still more produced beyond its proper suspensorial point; its *foot* or fork grows forwards over the mouth, and meets its fellow of the opposite side below the eye and behind the nasal sacs. Here we have the first rudiment of the "quadrato-pterygoid" arcade; it is found in the "maxillo-palatine" rudiment of the embryo. This is different from what is seen in the larval Frog at a similar stage ("Frog's Skull," pl. 3. figs. 3, 2, *mn*, & pl. 4. figs. 1, 2, *mn*), where the first postoral clings close to the *trabecula*. Afterwards, in the *third* stage, these bars, in the Frog, diverge; and then (fig. 7, *p.pg*) they become united by a conjugational band, the first rudiment of the large palato-pterygoid bar. Lying deeper within the tissues, in reality in the oral roof, we see the edge of a bar in the embryo Shark (Pl. XXXIV. figs. 1 & 6, *tr*); it is the trabecula.

The seven pairs of free visceral rods undergo a large amount of metamorphosis by segmentation, so as to form a most flexible oral and branchial apparatus. Already, over the infoldings of the young eye-ball, a ridge is seen; this is an important part of the skull when developed, namely the "superorbital band" (see "Salmon's Skull," pl. 4. figs. 1–3, *s.ob*). The ear-sac is still on the same morphological level as the nasal sac and the outworks of the eye-ball; it is a rounded fold, which soon will nearly close, however, and chondrify beneath the skin. The very rudimentary nasal sacs cleave close to the inferior surface of the depending fore brain. The mouth, notwithstanding the palatal foot-like process that passes over it, is very open and gaping; altogether the postoral bars and clefts make an "open-work" of the whole of the mouth and throat.

In the more advanced specimens (Pl. XXXIV. figs. 2–5), delicate thread-like

embryos nearly an inch in length, the skeletal tissues were acquiring a greater density, and the various folds of the skin were much more perfect. Yet over the third vesicle (C^3) the integument was quite transparent, and the contents of the head visible through it. A lateral view (fig. 2), seen by reflected light in a specimen hardened both by alcohol and chromic acid, shows how the skin is acquiring its proper characters in its growth from below upwards. The sense-capsule folds are closing; and the posterior edge of each postoral visceral arch has developed an opercular "vallance," the fringe from the second being the counterpart of that which is so largely extended backwards over the hinder arches (branchials) of the Osseous Fish. Here the free labiate edge grows from the mandible and gill-arches, as well as from the hyoid arch. Arrested at this stage, they would leave the gills much exposed; but they close in to a great degree, leaving only the well-known branchial slits. Morphologically considered, they also are the rudiments of such a growth of the skin as in an early stage covers over the visceral clefts in the "Abranchiata." No cartilage is developed at present in the substance of the mandibular arch at this part, merely a strong ligament which attaches the mandible to the skull between the trigeminal nerve and the apex of the hyoid arch. This ligament is the primary apex; the pterygo-quadrate is the secondary fork. A deep fissure is seen between the inturned end of the pterygo-quadrate bar and the olfactory sac (*na*). During growth the arcuate cleft between the first and second postorals has become a large triangular space, with the base above and the apex below. From the posterior edge of the upper part of the mandibular bar four clubbed filaments proceed; they look upwards and outwards: these are the free *external* transitory gills of the mandibular arch, the precursors of the pseudo-branchia. The counterparts of these, growing out of the succeeding arches, all but the last, are four or five times as long as in the more immature specimen. They are about ten on each bar, both on the right and left side. The lower and upper views of this specimen (figs. 3 & 4) are very instructive; and if the actual form of the enclosed bars of cartilage be held in mind (see fig. 1), it will be easy to understand their structure. The first cerebral vesicle (C^1) is completely beneath the second (C^2); and beneath the first the curious nasal sacs are seen, with their sigmoid valvular opening. The trabecular plate shows its form even in the opaque object. In front of the mouth are seen three lobes: the paired lobes contain the soft bulbous ends of the trabecular bars; and the azygous elevation between the nasal sacs contains the prænasal or basitrabecular cartilage, an unpaired *commissural* bar uniting the distal ends of the trabecular cornua. The solid side walls of the mouth contain not only the pedate pterygo-quadrate bar, but also the *fourth* upper labial cartilage; this will be shown better in a more advanced stage.

The lower jaw, seen from beneath, is a quadrilobate mass fixed behind and below by a broad short pedicle. Its external lobes are the angular and articular regions; and the submesial swellings contain the short *Meckelian* regions of this peculiar mandibular arch. The following arches are much more bowed out; and between them the visceral

clefts are more extended, both above and below; their edges also develop a more distinct opercular flap. The huge pharyngeal bag is now seen to be slit on both sides; six of these slits are developed, and they are partly filled in by a very beautiful growth of plicated skin and of long clavate filaments. These filaments, the external branchiæ, are now seen to arise from the hinder edge of the bars, and to escape from the clefts like the contents of dehiscing *carpels*. The *plicæ* are arranged like the cogs of a wheel; they occupy both sides of the first four branchial arches, the hinder side of the hyoid arch, and the fore edge of the last branchial. This open condition of the respiratory region of the œsophagus is temporary, but shows what is *possible* in a low vertebrate form; long before the embryo escapes from the horny tendrilled *pillow-case* the branchial slits are reduced to much smaller dimensions, relatively. The cog-shaped plicæ on these semicircular bars are the rudiments of the *permanent* or *internal* gills; they are hidden; and the bowed railings are filled in by the extension of the retral opercular folds. In the under view the umbilicus is shown, and on each side of it the rudiment of the pectoral fin; the heart is in the angular space between and below the posterior branchial arches, in front of the umbilicus. In the upper view, the ear-balls (*au*) are seen to be about the size of the eye-balls (*e*), and to be ovoidal in shape; they are beginning to acquire their own cartilaginous covering. The brain-sac is at present almost entirely membranous; and both the skin (cuticles and cutis) and the stratum of cells beneath that splits into dura mater and cartilaginous skull (roof and wall) are, in the upper region, exceedingly thin and diaphanous.

One of the most important views of the structure of this early stage of the Shark's skull is obtained by making a *solid* vertical section to be viewed as an opaque object (see fig. 5). Now the thinness of the integument over the third brain-vesicle (C^3) can be demonstrated; and this vesicle is largely filled by a thin fluid to two thirds its depth; the interior of the other vesicles is very soft and diffluent. The middle vesicle (C^2) is very bulbous; and the anterior (C^1) is now developing into the hemispheres. Above and behind the fore brain is the pituitary body (*py*); and it helps to enclose a space formed by the curvature of the neural axis at its cephalic end (mesocephalic flexure); this cavity in the hook of the *crozier* is filled with delicate gelatinous tissue; it is the transitory "middle trabecula" of Rathke. The notochord (*nc*) follows the elegant curves of the neural axis where it passes into the hind brain; it reaches to the pituitary body. On each side of the notochord is a subcartilaginous plate, the two halves of which form the "investing mass" (*iv*); beneath the investing mass lies the pharyngeal portion of the first branchial arch (*br*.1). This section well shows how the pharynx is railed in by the visceral bars, and that the mucous membrane is folded into a saw-like series, the *teeth* lying on the inner face of the bars above. The triangular opening ("spiracle"), corresponding to our tympano-Eustachian passage, is seen to be *high* and *short*, unlike its successors. The way in which the mandibular stem has been, as it were, trained forwards, like an espalier, to the front of the mouth, is also clearly shown.

To elucidate the meaning of the oral visceral arches more thoroughly, I have given a figure (Pl. XXXIV. fig. 6) of them in their earliest stage, separated from the rest, but shown in relation to the three infolded sense-capsules. Looked at unreflectingly, the mandibular and hyoid arches might be supposed to have their apex turned completely forward, so that the proximal part of the first might be brought to the distal end of the trabecular arch or plate; whilst the other, the hyoid, should have its apex close behind the *foramen ovale* (5). A careful observation of these, and comparison of them with those of the Skate (Pl. XXXIX. fig. 3) has satisfied me that the fore-turned hook is in reality a *secondary fork*, growing in these two arches from the primary fixing-point. Thus we still have the first position of the mandibular apex below the trigeminal nerve, and that of the hyoid below the auditory sac (*au*). Now, if the "third postoral" or first branchial be compared with these two, it will at once be seen that it has, like its successors, no fork, and that its apex corresponds with the heel of the foot-shaped top of the first and second bars.

We shall see, anon, what becomes of the pedate process, and of the proper apex from which it proceeds; the forked part is a "conjugational spur," having the same mechanical meaning as the slanting bars of a simple rural gate.

This stage is still further illustrated by a section which shows the floor of the rudimentary skull; it passes horizontally through the nasal sacs; but the eye-balls and ear-sacs are untouched (Pl. XXXV. fig. 5). The embryo which was thus prepared measured $1\frac{1}{12}$ inch in length—one sixth of an inch longer than the last.

The mesocephalic flexure was still perfect, the mid brain (C^2) being in front, and the fore brain (C^1) below; the highest part of this object is at the fore part of the notochord (*nc*), where it is embraced by the hind part of the trabeculæ.

Such a preparation, then, must be supposed to "dip" both in front and behind, from the postpituitary region; thus the trabeculæ (*tr*) and the investing mass (*i v*) meet at a considerable angle.

The skeletal parts here displayed are much less solid than the visceral rods. This is also the case in *Siredon* at a similar stage; but as the granular trabeculæ took up the carmine much more freely than the rest, and could be mistaken for no other tissue than young hyaline cartilage, I have coloured it as such.

But the cells forming the investing mass (*i v*) and the shell of the ear-labyrinth were much less coherent than those of the trabeculæ; and the internasal tract was still more behindhand in growth.

The huge swelling brain-sacs, especially the middle one (C^2), project far forwards; and traces of growth from the axis can be found as far forwards as the front of the elegantly plaited nasal sacs (*na*).

If the subcircinate series of structures in the head of this Selachian embryo be considered, it will be seen that there are three pairs of sense-capsules, and their inter-capsular regions, the auditory, the optic, and the olfactory interspaces.

But the hindermost of these is not segmented off at present from the rest of the axis; this part is composed throughout of two tapes of young cartilage, closely applied to the sides of a median rod—the notochord (*nc*)—whose diameter is one third of that of either lateral band (*i v*).

I have traced these structures back behind the inter-auditory region more than twice as far as that region extends, without finding any transverse segmentation answering to vertebral division: hence we are perfectly safe in assuming that the "basilar plate," or investing mass, is a continuation of the substance which in the spine makes itself into vertebræ [1].

The inter-auditory part of the investing mass has its sides bevelled and crescentically notched or concave; and the outer edges pass to some extent beneath the capsules. They do not reach further forwards than to the first third of the capsules, but are larger in the middle than at the sides, being inwedged between the ends of the trabeculæ and the notochord. They also pass a little beneath the trabecular plates in front; for, contrary to my earlier belief, I now find that the trabeculæ form the "posterior clinoid" region: in the Salmon ("Salmon's Skull," pl. 2. fig. 5, and pl. 4. figs. 2 & 3, *tr*, *i v*), the ends of the delicate trabecular band lie *over* the fore ends of the basilar plates.

The cephalic part of the notochord has not yet lost the bend downwards which is so conspicuous in early stages (Balfour, No. 2, pl. 24. figs. G, H, I); but it is much straighter than when first distinguishable.

At present, instead of ending in a hooked down-turned point, it ends in a beaded manner against the back of the pituitary body (*py*), which gets somewhat under the notochord which grows obliquely downwards and backwards (Pl. XXXIV. fig. 5, *py*).

The end of the notochord, where it pushes against the pituitary body, is vesicular; and behind this terminal swelling there are *six* more similar moniliform enlargements; the second and third are small, and lie in a twisted manner in front of the remaining *four*, which become as large in diameter as the even part of the rod (Pl. XXXV. fig. 5, and Pl. XXXIX. fig. 6, *nc*).

This beaded condition of the fore end of the notochord appears to me to be open to two interpretations: it may be a temporary subsegmented condition, corresponding to undeveloped or suppressed segments in the head; or it may simply be a puckering or folding of the sheath in a vegetative attempt to grow further forwards, the result of an effort to push away the pituitary barrier.

The interocular plates, or trabeculæ, are the parts hardest to be understood. They may be precociously solidified tracts of the same nature as the investing mass, having the notochord between them only behind, and their separateness due to a dislocation, as it were, the result of the mesocephalic flexure.

[1] Professor Huxley's term "parachordal" ("On *Menobranchus*," p. 198), for these paired bands, is not distinctive of them; for the terminal plates of the trabeculæ are also *parachordal*.

On afterthought, it is an anomaly to me that the foremost pair of visceral or "pleural" rods should grow straight forwards as the head straightens, and then from their upper edge develop three fourths of the chondro-cranium—namely the posterior and anterior sphenoidal regions, the ethmoidal or proper olfactory region, the internasal region in front of the tract supplied by the olfactory nerves,—and then finish off this exuberant and varied skull-growth by sending three prænasal "suckers" (the cornua and prænasal rod) into the intermaxillary region.

There must be here some suppression of originally distinct parts, or elements; and it seems to me now to be safer to give to the *axis* things that are axial, and to the *face* things that are facial.

The *axis* appears to me to pass insensibly into the *face* in the internasal region, although some may argue that even the trabecular cornua and prænasal rod are then productions of the fore end of the axial elements. The somewhat lyriform trabeculæ are of great breadth in the Selachians (compare Pl. XXXV. figs. 3, 5, 6, *tr*, with those of the Salmon, *l. c.* pls. 1–4).

In front they are shaped like pruning-hooks; the blunt hook looking towards its fellow behind the internasal tract, but not meeting it. The back of the blade looks forwards and outwards, lying close behind the olfactory sacs. Their interspace, which is largely occupied by the infundibulum and pituitary body (*inf*, *py*), is equal to their width. Behind, also, they do not meet, but apply their inner edge to the three foremost notochordal "beads" (Pl. XXXIX. fig. 6). They send a right-angled wedge between the front of the investing mass and inner face of the ear-sac, to which they cling, and in front of which they form a rounded elbow: hence the outer edge of each plate is deeply notched in a semioval manner. Externally, the front projection is the rudiment of the lateral ethmoid, the part to which the antorbital or ethmo-palatine cartilage is attached in some Selachians, in Teleostei, in Urodeles, and in Anura.

The hinder elbow is the part to which the "pedicle of the suspensorium" is attached in the Amphibia ("Frog's Skull," and Huxley on *Menobranchus*). The pterygo-quadrate ends in front immediately below the fore end of the trabeculæ; in front of the trabeculæ, between the granular nasal sacs, the internasal tract grows broad behind and pointed in front, the pointed tract being the rudiment of the azygous prænasal cartilage. The trabecular cornua are not at present solidified sufficiently to show their distinctness from the contiguous parts of the nasal capsules.

Second Stage. *Embryos of Dog-fish 14–16 lines in length.*

At this stage the embryo of *Scyllium canicula* still retains the "mesocephalic flexure," but the brain (Pl. XXXVI. fig. 2) has become very complex. The pituitary body (*py*) lies behind the fore brain (C^1, *a*), and the "middle trabecula" (*m.tr*) is not absorbed. The true trabecula (*tr*) is very much enlarged, and flattening out above and behind has begun to form the large flat floor on which the fore part of the brain-sac rests; the

edge of the outspread apex can be seen just above the pituitary body (*py*). At present the azygous basitrabecular rod is beneath the hemispheres (C^1, a); but afterwards it forms the axis of the beak or *cutwater*. On the whole, the sectional view of the second stage is much like that of the first; but a dissected head shows that changes of the utmost importance have taken place. The segmentation of the proper branchial arches will be shown better in the next stage; they all, save the last, break up into four pieces on each side—a "pharyngo-," "epi-," "cerato-," and "hypo-branchial" element. But the mandibular and hyoid arches (Pl. XXXVI. fig. 1, *mn*, *hy*) undergo only one transverse segmentation. This is but a step above what occurs in the Lamprey (Huxley, "Elem." p. 193, fig. 76, *g*), where the mandible does not become subdivided at all, and the hyoid arch is only severed across to form two pieces. Our next subject, the Skate, is far in advance of this; and on this point the ordinary Shark is not in advance of the *Chimæra*. It has recently been shown that in Osseous Fishes the hyoid arch is much more complex than its successors, the proper branchials ("Salmon's Skull," pls. 2, 3, 4, 5, 6 & 8), being composed of the same number of cartilages; but three of these are partly segmented, each into two, by having an additional bony centre. In the Sturgeon ('Monthly Microsc. Journ.' May 1873, pl. 20. fig. 1) there are *five* cartilages on each side. Here, then, the "pharyngohyal" and the "epihyal" are in one piece, and the "ceratohyal" and "hypohyal" are in one. Here also the *mode* of segmentation is different and altogether simpler: in the bony fish it is from top to bottom, the second postoral bar being longitudinally segmented ("Salmon's Skull," pl. 2. fig. 3); but in the Shark it is *transverse* segmentation, exactly like that of the bar in front, namely the mandibular. Whilst the pedate process of the mandible runs and fastens itself to the trabecula by its apex, the hyoid applies its pedate process to the whole side of the auditory capsule on which it is hinged; but the distal part of the upper piece is strongly tied to the arch in front of it. This simplicity of the oral arches occurs in the "Dipnoi," and also is the pattern on which the "Urodela" are constructed, although in both these cases fibrous bones complicate the structure; but in the Teleostei, as a rule, and in Ganoids, both "Chondrostei" and "Holostei," the oral arches have to be traced up from those of the Rays, which are complex; these are to be described presently.

Whilst the apex of the hyoid arch as well as the pedate process keeps attached above, the apex of the mandible becomes a mere fibrous band in front of the "spiracle," or first postoral cleft. This band is attached to the skull behind and below the fifth nerve (fig. 1, *cl.* 1). Here is the beginning of that peculiar modification of the Fish's skull by which the mouth becomes so mobile, the mandibular and hyoid arches hanging from the head by a single suspensorium—the "hyomandibular,"—which may be either the *whole* of the upper part of the hyoid arch, as in the present instance, or the larger *half* of it, obtained by longitudinal segmentation, as in the Salmon ("Salmon's Skull," pl. 2. fig. 3, *h.m*).

The most advanced specimens at this stage (1 inch 4 lines long) show much that is instructive, and fairly bridge over the space between the first and third stages.

The head is fast becoming straight—see the nearness of the fore margin of the nasal sacs to the front of the head (Pl. XXXV. figs. 6, 7, as compared with fig. 5); and the trabeculæ, investing plates, notochordal sheath, auditory capsules, and visceral arches are all now chondrified.

In a horizontal view of a preparation in which the nasal and optic capsules were cut through, and the brain all removed, except in front (Pl. XXXV. fig. 6), we get a good view of the foundations of the Selachian chondrocranium.

The notochord, which with the investing mass that has been cut through at some distance behind the auditory capsules, is enclosed in a strong sheath of hyaline cartilage, has lost its beaded character in front, and now has pressed its end flat against the back of the pituitary body.

The halves of the investing mass are scooped along their inner edges, where they cling to the sides of the notochord. Each plate passes some distance below the auditory capsule, but much more at both ends than in the middle. These cartilaginous bands have coalesced with the trabeculæ in front, growing into the lower edge of the thick transverse postpituitary wall (*p.cl*, *py*, *iv*, *tr*).

The auditory capsule inside the anterior ampullar enlargement has coalesced with the thick outer end of the posterior clinoid wall. In front of the wall the trabeculæ dip, and are somewhat concave; behind, directly in front of the ear-capsules, each trabecula is growing upwards into an alisphenoidal crest, which runs forwards to the optic nerve (2). This is their narrow part; further forward they expand behind the nasal sacs in a pedate manner, but do not yet meet at the mid line.

The intertrabecular space is larger than its enclosing cartilages, and is only occupied at its end by the neck of the pituitary body.

At the mid line, between the trabeculæ and the olfactory sacs, the granular semi-cartilaginous internasal tract is seen. I cannot discover that the tract is ever divided into two distinct bands of cartilage, although its counterpart always is so divided, *below*, in the Amphibia; in front it widens, curves right and left round each nasal sac for some distance, and in the middle sends forward an azygous rod.

This latter is the prænasal rostrum, the axis of the "cutwater;" and the lateral growths are the cornua trabeculæ. Each of these is bilobate; and in the next stage we shall see what a curious modification these two projecting masses of cells have undergone.

At present it should be noted that the olfactory sacs, whose dome-like roof is now fast changing into cartilage, are very close together, only leaving a narrow valley between them, and leaving scant room for the septum or internasal region of the trabeculæ.

When the head is examined from below we see the free forward growth of the

suspensorium; a complete separation of the upper from the lower part of the strongly bowed mandibular rod has taken place; but the pier, instead of growing upwards as a cartilaginous "pedicle" to be attached to the trabecular elbow, as in the Amphibia, is merely fibrous upward; and the cartilage grows a far way forwards, even to the olfactory sac, and then turns almost directly inwards to form a junction with its fellow, as in the free jaw below (Pl. XXXV. fig. 7, *qpg*, *mk*).

At present the free jaw-pieces are thick where they are scooped in their articular region for the quadrate condyle, but they lessen gradually to the chin; their direction is forwards and somewhat downwards.

The next or hyoid arch has its sides subdivided in the same manner as the mandibular; there is one transverse cleft a little above the middle, dividing the bar into an epi- and a cerato-hyal; here, however, the scooped face is on the upper and the rounded head on lower segment.

The upper piece does not quite correspond with the hyomandibular of the Osseous Fish, where the primary bar is split down from top to bottom; here it is merely divided by a sinuous cleft. A shield-like plate, the basihyal (*b.hy*), unites the two lower pieces under the throat. The upper piece, called, ichthyotomically, the hyomandibular (*h.m*), has a broad top, which is applied closely to the inferolateral region of the ear-sac (*au*). At its middle in front it becomes angular, and is strongly attached to the arch in front.

The proper branchial arches have a part that runs under the hind part of the head and neck, that is separately chondrified; this is the pharyngo-branchial piece (*p.br.* 1); it is turned backwards and inwards. There is also a division of the bar into an epi- and ceratobranchial (*e.br*, *c.br*); and afterwards there will be a hypobranchial piece below. These things will be best seen in the next stage.

At present the four external branchial filaments growing out of the "spiracular opening" are one third the length of the exceedingly long clubbed threads that break from the second cleft (fig. 6, *e.br*). They are all clubbed at the free end, where the single capillary loop turns back again to the main vascular arch.

After the time of this stage the embryo grows much faster in bulk than in length; the snout becomes like that of the adult (Balfour, *l. c.* pl. 25. figs. P, Q); the cartilaginous side walls and roof of the cranium chondrify at a rapid rate; also the facial rods become fully segmented and their metamorphosis fairly completed.

Third Stage. *Embryos of Dog-fish* $1\frac{1}{2}$–2 *inches long.*

The Dog-fish has fairly undergone its metamorphosis at this stage, although there are many important points to be noticed, in which the parts differ from the state of things in the adult; this is largely a matter of *relative size.*

The mesocephalic flexure is lost (Pl. XXXVI. figs. 3–6), and the "median trabecula" (fig. 6) is now a mere fissure between the medulla oblongata and the mid brain. The

large and complex brain well fills the flat oblong brain-cavity, *in front* of which we now see the exquisite folds of the nasal sac (*ol*).

Looking at the basis cranii (Pl. XXXVI. fig. 6, and Pl. XXXVII. fig. 1), we find that the notochordal region is now a broad subquadrate tract of cartilage, the two moieties of which have coalesced; there is a very small cone of gelatinous tissue left.

The investing mass (*i v*) behind is developed into two lobes for articulation with the "atlas;" and in front its extremities are rounded, the whole basilar palate being emarginate in front. This emargination and the space between the præpituitary cartilages (*tr*) make together a *thin* subpituitary space of cartilage of a lozenge-shape. The "internal carotids" (*i. c*) pierce this space at its broadest part. Opposite these passages the anterior pair of cartilages (*tr*) curve outwards into a short flat cornu. This cornu is the "elbow" of the trabecular bar (*tr*); it is largely separated from the side of the basis cranii, being bowed out: this is well seen in the Porbeagle (*Lamna cornubica*), and also in *Carcharias glaucus* (see "Huxley and Hawkins's Atlas," pl. 5. fig. 4). In the basal figure of this skull of the embryo Dog-fish (Pl. XXXVII. fig. 1, *tr*) the trabeculæ are seen to be of great size and remarkably flattened out; they expand beneath the eyeballs, and send out an antorbital process on each side. In front of these processes the trabeculæ are suddenly narrowed, and end between the nasal sacs (*na*) in a pair of short horns (cornua trabeculæ, *c.tr*). These are the distal extremities of the trabeculæ, which here have a basal or azygous piece, the prænasal rostrum or "basitrabecula" (*b.tr*). This is exactly like what has been described in the Bird ("Fowl's Skull," pls. 81–84, *pn*); its direction is a gentle curve upwards (Pl. XXXVII. fig. 4, *b.tr*).

The trabeculæ at their extremities are 4-winged in section; for the narrowed thick lower part sends upwards, but more outwards, a thin broad lamina (Pl. XXXVI. figs. 3 & 4; Pl. XXXVII. fig. 1, *c.tr*); this is the "trabecular crest," and is a very important structure. In vertebrates with high skulls and a well-developed meso-ethmoid (perpendicular plate and nasal septum), the nasal sacs come close together, and their inner plates not only coalesce with each other, but also with the ascending trabecular crests, to form the single solid septal plate.

Here the distance of the olfactory sacs from each other leads to the correlated divergence of the trabecular crests, which coalesce with the inner walls of the nasal dome. Each outspread crest gives off a small sigmoid cornu; and these two horns curl inwards towards the basitrabecular rostrum. To help in the interpretation of these parts the nasal domes have been emptied of their olfactory folds, and the valvular "labials" turned a little aside (Pl. XXXVI. fig. 4, and Pl. XXXVII. fig. 1, *na*, *l*, 1, 2, 3).

The dome-shaped olfactory cartilages are not only joined by coalescence to the trabecular crests; they are also confluent with an important pair of cartilaginous bands, namely the superorbital tracts of cartilage; these have already been described in the Salmon ("Salmon's Skull," pl. 4. *s.ob*), and are well shown by Dr. Traquair in the *Polypterus* (Journ. of Anat. and Phys. vol. v. pl. 6. figs. 2 & 3). They are early seen

as thickenings over the eye (Pl. XXXIV. figs. 1 & 2, *s.ob*, and also in the Salmon, "Salmon's Skull," pl. 1. figs. 1, 3, 6 & 7). We thus come to a proper understanding of the nature of the ecto-ethmoidal masses of the higher vertebrata; they are composed of the proper olfactory domes, and the superorbital bands, which reappear in front beneath the nasals and frontals at their contiguous edges ("Fowl's Skull," pl. 83. figs. 2 & 5, *al.e*). The extreme simplicity of these primordial olfactory capsules (they send no outgrowths between the folds of the Schneiderian membrane) makes them of great use for unlocking the difficulties in the higher types, where several *regions* are specialized and many outgrowths formed.

In the Shark there is no "fontanelle" proper; but the roof of the cranium ("tegmen cranii") ceases in front, close to the nasal sacs (Pl. XXXVI. fig. 3, *t.cr*, *na*), so that the cranial cavity is open in front, and the long rhimencephalic crura diverge and pass into the nasal region beneath the inner side of the dome (fig. 4). These nervous masses lie on the trabeculæ, and escape into the nasal sac through a space formed between the inter-nasal region of the trabeculæ and their olfactory cornua (*c.tr*); this "fenestra" answers to the chink in the Bird and to the cribriform plate in the Mammal. The diverging crests of the trabecular cornua (figs. 3, 4) being so outspread, the "olfactory fenestræ" are in this stage nearly horizontal; but in the adult (Pl. XXXVII. fig. 3. 1) they are slanting, their direction being upwards and forwards from the narrowed trabecular bar to the postero-superior margin of the olfactory dome inside. Looking at the beaked face of a large shark, such as the Porbeagle (*Lamna cornubica*), it does not at first seem evident what the two clumsy-looking rods of cartilage are that converge towards the end of the basitrabecular rostrum. In the present subject (*Scyllium*) they are flat bands burrowed by slime glands (Pl. XXXVII. fig. 3, l^1). In this early stage they are easily interpreted (Pl. XXXVI. figs. 3, 4, 5, and Pl. XXXVII. fig. 1, l^1, l^2, l^3); they are two of the labial ("extravisceral") cartilages that cluster round the large nasal opening, to which they are related as valvular folds.

The second and third of these are applied closely to the edges of the dome. The second is in front; and this is of a crescentic shape; it enlarges the nasal cavity, and partly floors it. The third is a thick ear-shaped cartilage on the outer edge of the nasal dome; this is the "appendix alæ nasi" of human anatomy.

The first of these cartilages is in front of the second; it is somewhat heart-shaped, and slightly overlaps the second; already it is the recipient of the two or three slime-glands which have burrowed its upper surface (Pl. XXXVI. fig. 3, l^1). Afterwards it reaches over the nasal dome, and contains many glands (Pl. XXXVII. fig. 3, l^1). The fourth labial (Pl. XXXVI. fig. 4, l^4) is lanceolate with its stout end forwards; it underlies the quadrato-pterygoid bar (*q.pg*), and lies on the upper edge of the angle of the mouth. A similar cartilage, converging towards the last, lies on the lower edge of the angle of the mouth, attached to the infero-lateral surface of the mandible. This is the *fifth labial* (Pl. XXXVI. fig. 4, l^5). Similar cartilages, "extrabranchials" (see

Pl. XXXVI. fig. 4, *ex.br*), appear outside each of the gill-bearing branchial arches, four on each side, making in all *nine* pairs of these external cartilages. Three fourths of the space between the superorbital bands is filled up by the gently convex cranial roof, "tegmen cranii," which reaches as far as to the superoccipital (*s.o*), covering in the whole of this flat-bottomed boat as with a slightly shelving *deck*. Between the trabeculæ below and the superorbital above, there is a cartilaginous wall, reaching from the ear-sac to the nasal sac; this is the sphenoidal wall, and answers to the orbitosphenoid and the alisphenoid of the higher vertebrata. A sectional view (Pl. XLII. fig. 5, *o.s*) shows how the cranial walls are chondrified, thickened above by the superorbital band, and below by the trabeculæ; each of these regions of cartilage gives off a wing, the upper wing roofing the eye-ball, and the lower forming a partial floor for it.

The optic nerve (2) divides the orbital ala from the "ala major"—that is, regionally. A primordial fissure between the alisphenoidal cartilage and the auditory sac (*au*) is converted into a crescentic foramen, the "foramen ovale" (Pl. XXXVI. fig. 5. 5). Where the superorbital cartilage, grafted on to the nasal sacs, becomes *præorbital* (Pl. XXXVI. fig. 5), we get the meaning of the lower part of the ecto-ethmoid, or pars plana, of human anatomy. The nasal branch of the ophthalmic nerve (5^1) passes between this downgrowth and the cranial wall.

The hinder part of the flattened cranial floor (Pl. XXXVII. fig. 1, *i v*) is formed by the investing mass, and is the *notochordal* region. It reaches from the foramen for the internal carotid to the occipital condyles (*oc.c*). Sectional views, the one (Pl. XLII. fig. 6) in front, and the other (fig. 7) behind, show the degree of its downward convexity, and its thickness at either end. The notochoid (*nc*) is still present in the hinder section; it is very small, and imbedded in the very substance of the cartilage; its *cartilaginous* sheath has coalesced with the lateral plates. The originally oval auditory sacs have taken the form of their bulging contents, especially of the large semicircular canals, which are very evident to sight on the upper surface (fig. 3, *a.sc*, *h.sc*, *p.sc*).

The cartilage is complete both on the inner and outer sides, save where nerves and vessels pass (Pl. XLII. fig. 6) through the anterior part of the capsule and (fig. 7) through the posterior part. The capsule has coalesced with the superorbital band in front and above, with the superoccipital and tegmen cranii supero-mesially, and with the investing mass below. The hyomandibular is articulated below the horizontal (external) semicircular canal.

The changes that have taken place in the first postoral (mandibular and pterygoid) are remarkable. The true apex, or metapterygoid (fig. 3, *sp.c*), is a fibrous band with a grain of cartilage in the anterior lip of the first cleft, or "spiracle." The descending bar sends forwards an enormous foot, the pterygo-quadrate bar; and the descending part is cut off from this, as the free mandible or articulo-Meckelian rod (*q.pg*, *q*, *ar*, *mk*). Thus the *secondary arch*, or pterygo-quadrate, becomes practically as strong a bar in front of the mouth as the lower part of the arch behind it. That nearly the whole

apparatus of the upper jaw and palate of a Selachian should be developed out of a pair of *processes* growing forwards from the primordial mandible, seems at first sight a most unlikely thing; and yet no fact in morphology has been better established.

The clue to its discovery was the peculiar segmentation of the primary hyoid arch in most vertebrates, either very obliquely through the upper third or half, or even, as in the Salmon, fairly from top to bottom longitudinally, the upper segment in this case generally growing forwards as a conjugational bar, yoking the hyoid on to the mandibular arch. Here, in the Shark, the primary and the secondary arches of the mandible (Pl. XXXVI. fig. 4) are extremely alike both in form and size, and are specialized to form this kind of mouth very perfectly. The halves of both meet at the middle, and are conjoined by a strong ligament; sinuous, flat, and selvedged for the greater part of their extent, they become terete and incurved distally. The articular region is gently scooped for the quadrate condyle; this is better seen in the side view of the adult skull (Pl. XXXVIII. fig. 2).

The very simple hyoid arch (Pl. XXXVI. figs. 3 & 4, *h.m*, *c.hy*, *b.hy*) is a solid structure; the suspensorial part is morphologically a *whole* "epihyal" piece, with no pharyngohyal segment above, and articulating with a "ceratohyal" from which no "hypohyal" element has been cloven; the right and left bars meet by the intervention of a very elegant flat broad keystone piece, the "basihyal" (*b.hy*), which has a convex anterior and concave posterior margin.

In this extremely mobile face only one more keystone element is found, namely the "basibranchial;" and this belongs to the last two arches. The branchial arches, five in number, are very uniform on the whole; and the great development and singular uniformity of these arches in the "Elasmobranchs" makes them fairly typical as to the segmentation of this class of arches throughout the Ichthyopsida. Although the basal piece is only developed in relation to the two hindermost arches, yet the two in front of these have their distal symmetrical segment attached to that piece; thus, functionally, it serves for four arches. Each arch has three fibrous joints on each side, developed in the original substance of the joint by a limited production of connective fibrous tissue instead of hyaline cartilage. Each bar, in its primary form, is very elegant: it is bowed out laterally; it descends in a sloping manner forwards; and both its apex and its distal end are hooked backwards, these hooks becoming the "pharyngobranchial" and the "hypobranchial" elements (Plate XXXVI. figs. 3 & 4, *p.br*, *h.br*). The upper third of the main bar, answering to the hyoid suspensorial piece, becomes the "epibranchial" (*e.br*); and the remainder is the proper ceratobranchial (*c.br*).

In the first branchial the hypobranchial is a small nucleus cloven from the anterior lobe of the foot-shaped extremity (fig. 4, *h.br*, 1); but in the rest of the functional arches the hypobranchial is a typical segment—large, free, and retrally attached to the base of the ceratobranchial.

The pharyngobranchial of the fourth arch belongs also to the fifth (fig. 3); forking below, it is attached to the apex of both the fourth and fifth. This latter arch has its epibranchial continuous with the pharyngobranchial of the fourth; it has a flat notched ceratobranchial piece (fig. 4, *c.br*, 5), and has no hypobranchial.

The sectional views further illustrate this stage of nearly ripe embryos of the Dog-fish.

A vertically longitudinal section (Pl. XXXVI. fig. 6) shows how completely the cranial cavity is filled with the brain, and that the mesocephalic flexure is obliterated. The tegmen cranii is continued over part of the fore brain; and the floor of the cranium is one continuous sheet of cartilage, formed by the investing mass behind, and by the united trabeculæ in front. The nasal sac (*ol*) now lies in front of, as well as somewhat beneath the fore brain. Beneath and behind the olfactory folds is seen the distal end of the pterygoquadrate bar (*q.pg*), and below the mouth the distal end of the mandible (*mn*). The hyoid crus and base (*c.hy*, *b.hy*) and the distal parts of the branchial arches are shown, as also the basihyal and basibranchial, in section (*b.hy*, *b.br*). There is but little of the notochord (*nc*) left; and a posterior clinoid ridge shows the rudiment of the "sella turcica." The pituitary body (*py*) is very small; beneath it the internal carotid is seen entering the cranium.

In the first of the transverse sections (Pl. XLII. fig, 5) the eyeballs are cut through, and a view is gained of the height and width of the cranium, built upon the foundation of the trabeculæ and their "commissure." The orbitosphenoidal side walls connect the trabecular crest with the superorbital band and the "tegmen cranii." Below the mouth (*m*), the oral "labials," the pterygoquadrate bands, the mandibles, and the fore part of the basihyal are cut through (*q.pg*, *mn*, *b.hy*).

In another section further backwards, and somewhat oblique (fig. 6), the hinder part of the eyeball (*e*) and the fore part of the auditory sacs are shown. The basal cartilage is cut through where the trabeculæ have coalesced with the investing mass. The third section (fig. 7) is through the posterior and horizontal semicircular canals (*p.sc*, *h.sc*), the upper part of the oblique foramen magnum (*f.m*), the investing mass, and remnant of the notochord (*iv*, *nc*), and the head of the hyomandibular, or "epihyal" (*h.m*). The thick auditory capsule is seen to be still distinct above from the superoccipital cartilage (*so*). The passage for the glosso-pharyngeal and vagus (9, 10) is seen below.

The remarkable extravisceral cartilages (Pl. XXXVI. fig. 4, *ex.br*) are shown outside the branchial arches: they are sharp above, and dilated below; there are four pairs of them; and the last (*e.vs*, 9) is very small.

These cartilages await proper classification; at present they may be bundled up with the "labials."

Fourth Stage. *Adult Dog-fish* (Scyllium canicula).

At first sight it might be supposed that a skull without any proper ossification in the adult state would present the greatest difficulties to the morphologist; for the various elements of the cranium are here thoroughly soldered together, making a com-

plex cartilaginous box, as complete as the bony box seen in the skull of the higher kinds of birds. Here, if anywhere, the cranial segments *ought* to be found. But, morphologically, these types are not at a very low level; certainly, if the cranium, even behind the pituitary body, be the result of slow *secular* consolidation of a series of vertebræ, these fishes would seem to be a very late product of evolution.

The truth of the matter is, that the Sharks and Rays are very enigmatical as to their position in the vertebrate series; below the Teleosteans as to their skull, by two important steps or degrees (as was shown in the paper on the Salmon's skull), they yet come much closer to the tail-bearing and tailless Amphibia than any other fishes with the exception of the "Dipnoi."

These things must be borne in mind whilst studying the conditions of the adult skull of a type which undergoes no bony metamorphosis, yet has so very perfect a cranium and a large and perfect basket-work of visceral arches.

The cranium itself (Pl. XXXVII. figs. 2, 3, Pl. XXXVIII. figs. 1, 2) is a very elegant structure; it is a flat-bottomed barge, like that of the frog ("Frog's Skull," pl. 9. figs. 6 & 7), but having a cartilaginous deck. On each side, in front, there is an elegant dome-shaped "awning"—the roof of the nasal sac; the *deck*, or tegmen cranii, is wide open in front; beyond this opening a small "prow" projects, the "prænasal or basi-trabecular" cartilage; and this is spliced obliquely by a pair of bars, the foremost extra-viscerals, which were in front, simply, and now overlie the nasal roofs (Pl. XXXVII. fig. 2, *l.* 1).

The basal view (Pl. XXXVII. fig. 3) shows the almost uniform breadth of the whole of the occipital and sphenoidal regions, the centre of the post-sphenoidal territory being shown by the entrance of the internal carotid (*i.c*). The occipital condyles (*oc.c*) project but little; the ridges of the otic capsule square the skull behind; and these ridges form a "tegmen tympani," under which there is no tympanic cavity, but a condyloid subconcave facet for the huge representative of the incus, the "epihyal" or hyomandibular. The lower edge of that facet is formed by the investing mass (*i v*); between this and the flat, outspread trabecular elbow (*p.tr*), is a notch; and a lesser notch separates the elbow from the rest of the trabecular plate, which further forwards narrows again, and then sends out the antorbital spur (*a.o*). The trabeculæ then suddenly contract, and grow upwards (Pl. XXXVII. fig. 3); and their ascending part becomes now coalesced with the inner edges of the nasal-roof cartilages, thus forming a primordial mesethmoid or septum between the nasal sacs, which is normally composed of four cartilaginous growths. On each side of this middle wall a membranous space, open in the middle, forms a sort of trap-door down into the nasal sacs, through which the olfactory fibres pass to the nasal plicæ, which are pinnately arranged, and entirely membranous. These spaces answer to the moieties of the cribriform plate of the mammal. The second labial (*l.* 2) has partly coalesced with the anterior edges of the nasal dome, and with the corresponding cornu trabeculæ (*c.tr*). The third labial (*l.* 3) is precisely like

that of the pig ("appendix alæ nasi"), and protects the outer edge of the lip of the nasal sac (see "Pig's Skull," plate 36. fig. 1, *ap. a.n*). Seen from above (fig. 2) the skull is a very elegant structure, with its approximated nasal roofs, its prow-like trabecular rostrum (*b.tr*), its oval anterior remnant of the fontanelle, and its convex tegmen cranii. The superorbital ridges (*s.ob*), so early seen in the embryo, now give character to the skull; they are grafted upon the otic capsules behind, and upon the nasal capsules in front, and even down in this type complicate the morphology of the ectethmoid. A superorbital foramen opens out in the front part of the groove between the superorbital and the "tegmen;" and behind the tegmen are seen the right and left "aqueducts of the vestibule" (*aq.v*). On each side of these the elevation caused by the semicircular canals is clearly seen.

A lateral view (Pl. XXXVIII. fig. 2) shows the relation of the parts very clearly, and especially lights up the wing of the "antorbital," or "pars plana." Although in the bird and mammal the antorbital cartilage is absent over the eye, yet it appears behind in the "sphenotic" region of the otic cartilage, and in front on the lateral ethmoid, running down in front of the eye as the free outstanding edge of the ectethmoid ("Fowl's Skull," plate 81. fig. 5, *p.p*), whilst the "tegmen cranii" reappears as the retral spike growing from the coalesced nasal sacs (ibid. plate 83. figs. 2, 4, 5 (*eth*).

Here there is no distinction of orbital and larger wings of the sphenoid; the space between the superorbital and trabecular cartilages is filled in by a continuous growth of the same nature—a vertical sphenoidal wall, which is riddled with larger and smaller holes, the more important of which serve as landmarks for morphological territories (Pl. XXXVIII. figs. 2 & 4. 2, 5, 5^1).

Besides the olfactory fenestræ, there is another between the partially fused trabecular cornua and nasal roofs (Pl. XXXVIII. fig. 4, *tr.f*). The mammals do not show this; but in birds it is very common—a re-separation of the trabeculæ from the nasal *inner* walls; it is not seen so low down as among the true "Struthionidæ" ("Ostrich's Skull," plate 7. fig. 2, *s.n*)—but appears in the next group, the Tinamous (ibid. plate 15, fig. 8, *s. n*), and in the Fowl in the *Tinamine* stage. ("Fowl's Skull," plate 83. fig. 4, *c.f c*).

The Mammalian skull is markedly prefigured by that of the Shark in the pituitary region; there is an anterior and a posterior "clinoid wall," and a floor to the sella turcica perforated on each side by the internal carotid (Pl. XXXVII. fig. 5, *a.cl*, *p.cl*, *py*, *i.c*). This is quite unlike what is seen in Osseous Fishes, Lizards, and Birds, which have no cartilaginous floor to their "sella." The notochord is replaced by cartilage; and the articulation of the skull to the "atlas" is by two condyles.

Between the superoccipital cartilage and the proper tegmen cranii above there is a crescentic fossa, looking forwards; on each side of this is the aqueductus vestibuli (Pl. XXXVII. fig. 2, *aq.v*).

On each side of these burrowings are seen the anterior and posterior semicircular canals, the latter ending in the epiotic eminence. Outside the ampulla of the

anterior canal is seen a short thick process, the sphenotic process (*sp.c*): it is formed by the grafting of the superorbital arc (*s.ob*) on to the auditory mass. Behind the notch is the large "pterotic" eminence (*pto*), containing the horizontal canal (*h.s.c*). Whatever the superorbital arc may be morphologically, it is a structure of the greatest importance; here, at its fullest growth, it shows that the "lateral ethmoid" and the periotic capsule are made *compound* by coalescence with it; and this original composition of these parts must never be forgotten in an ascending survey.

Thus the nasal capsules are mixed up, or confluent, with the trabecular and basi-trabecular bars, with the superorbital arcs, the "tegmen cranii," and one pair at least of the labials. The periotic capsule is fused with the "parachordal" bands, or investing mass, with the arch growing upwards from that mass (occipital arch), with the tegmen cranii, and with the superorbital arc.

Afterwards, when we come to study such skulls as have the chondrocranium ossified into certain definite (interneural) bony territories, we shall often see a single bone formed in what was a very complex part originally; and therefore such bones must be considered as the products of metamorphosis, and not primordial elements of the cranium.

A section taken longitudinally (Plate XXXVII. fig. 4) shows how the brain ($C1$, $C1a$, $C2$, $C3$) fills the cranium, and how the occipital ring and tegmen cranii cover the greater part of the brain. Below, the notochord only persists between the atlas and the basis cranii; further forwards the internal carotid (*i.c*) is seen entering the skull-base below the sella turcica (see also fig. 5), which has an anterior and a posterior clinoid wall (*a.cl*, *p.cl*) and contains the tear-shaped pituitary body, above and in front of which is the hollow infundibulum (*inf*).

In front the mesethmoidal *fenestra* (*tr.f*) is seen to be a mere membranous space where the nasal sacs have not thoroughly coalesced with the trabeculæ; in birds this fenestra is formed by the *reopening* of the cartilaginous wall after complete fusion has taken place.

When the brain has been removed, the various openings can be seen for the exit of the nerves: these lie low down; and the chiefest of them can be easily determined (see Pl. XXXVIII. fig. 4. 1, 2, 5, 7, 8, 9, 10). That for the olfactory (1) is a large obliquely tilted window—the membranous "cribriform plate."

The chondrocranium is not more massive and complete than the facial or visceral arches, which here attain their utmost size, and undergo no further histological meta-mophosis than the calcification, in tesseræ, of the superficial cells of the hyaline cartilage. Arrest in metamorphosis (as to bony deposit) is here the correlate of large development of the parts as to size; in *number* this and many other sharks agree with the Osseous Fishes, there being seven postoral arches; there are more in *Hexanchus* and *Heptanchus*, which have respectively six and seven persistent branchial slits, besides the "spiracle."

The pterygo-mandibular arch (Pl. XXXVII. fig. 2, and Pl. XXXVIII. figs. 1 & 2, *q.pg*, *q*, *mn*, *mk*) is curiously swung from the outside of the basis cranii by two short ropes of fibrous tissue: the hindermost of these is the true apex of the arch, the metapterygoid, or " pedicle " (*l*, *sp.c*); and the foremost is the palato-trabecular conjugation (*p.tr*). This latter is attached to a process on the pterygoid, too short to reach the trabecula; and the metapterygoid band in front of the spiracle (*cl.* 1) is attached above to the skull, close in front of the hyomandibular (*hm*), and behind and below the fifth nerve (5). Where this band is attached to the quadrate region (*q*), the cartilage is bevelled down, only sufficient substance being left to form the condyle for the mandible.

There is, however, but little difference in size between the upper and lower jaw-plates; for the upper broadens as it arches upwards to the dentigerous part, and then it gently curves downwards to its pterygoid or distal end, which is strongly tied by a ligament to its fellow of the opposite side. This bar is bowed out at its upper margin, as is the mandible at its lower edge; the scooped surface thus formed gives attachment to the oral muscles. This *primary* mandible has a very similar form to the *secondary* mandible of a mammal, save in not possessing a coronoid process. Its narrowing dentigerous part is equal in size and extent to that of the upper bar; the right and left halves are similarly bound together by ligamentous fibres.

The hyoid arch is as simple as the mandibulo-pterygoid, being composed of two pieces only; the whole arch cleaves close to the one in front, and is locked within it below. This is a foreshadowing of what takes place in more metamorphosed types, as is also the suspension of both the free crura from the pier of the hyoid, which now can fairly be called, from its function, the hyomandibular (*hm*). The metapterygoid ligament is attached below equally to the two contiguous condyles—namely, that of the quadrate and of the hyomandibular; thus the weight of the large mandible is transferred largely to the hyoid pier. The hyomandibular has a joint-cavity above and below it; and its articulation with the free cornu below is like that between the human finger-joints.

The thick, ribbed, outturned edge of the mandible is attached at its rounded angle, near the joint, by a strong " mandibulo-hyal " ligament (*m.h.l*), as in the Urodeles; in Osseous Fishes the angular ligament becomes bony above, as the " interopercular." The stout phalangiform ceratohyal (*c.hy*) by this ligament is kept close to and within the mandible; it is bilobate distally; and the anterior lobe articulates with the angle of the elegant heart-shaped basihyal (Pl. XXXVIII. fig. 1, *c.hy*, *b.hy*); there is the merest rudiment of a joint-cavity at this part, but, as in the arches behind, a profusion of fibrous tissue.

As the hyoid arch is functionally branchial, it carries branchial rays (*br.r*), that give strength to the pouches. There are three of these on the hyomandibular, the upper of which is trifurcate, the middle bifurcate, and the lower subdivided into five or six long leaflets.

On the ceratohyal (Pl. XXXVIII. figs. 1 & 2, *c.hy*, *br.r*) there are seven, the upper of these being quinquefid, and the rest bifid. The branchial rays on the next four arches (the principal branchials) are simple in form, and range in number from ten on the first to five on the last. Two or three of these are on the "epibranchial," the counterpart of the hyomandibular, and the rest on the ceratobranchial."

The hyoid arch meeting with the chondrocranium, and articulating with it, has no "pharyngo-pleural" element, a part developed in all the succeeding bars, which float, as it were, over the large pharyngeal cavity, and are not attached to the axis of the animal.

The branchial arches (Pl. XXXVII. fig. 2, *br*, and Pl. XXXVIII. figs. 1 & 2, *br*) are, on the whole, very uniform; but the fifth, or last, is abortively developed; on it, as on the hyoid, there is but one series of branchial plicæ. These arches have great mobility, and form complete girdles to the huge pharynx; their apices meet together above, and their distal parts below; behind, there is a large keystone piece to the last two of the arches (Pl. XXXVII. fig. 2, and Pl. XXXVIII. figs. 1 & 2, *b.br*). Having great mobility, the dorsal segments (pharyngo-branchials, *p.br*) *may turn forward* (Pl. XXXVII. fig. 3, and Pl. XXXVIII. fig. 2), or backwards (Pl. XXXVIII. fig. 1); normally they turn *backwards* [1], the opposite direction to that taken by the hyoid and mandibular arches. Nevertheless the segment that corresponds with the upper part of those arches, namely the epibranchial (*e.br*), sends forward a *pedate process*, the exact counterpart of the fore part of the head of the hyomandibular, and of the quadrato-pterygoid lobe of the mandibular arch. The pharyngobranchials are thus seen to be attached behind the pedate process, which is what occurs in the hyoid of the frog, where the pharyngohyal element ("interstapedial") is developed on the end of the hinder fork of the bar. Primarily the direction of the dorsal ends of the visceral arches is inwards and backwards, and the foreturned part is a secondary spur or fork; the ventral or lower ends have also a retral habit of growth; so that normally the hypo-pleural element is always more or less hooked backwards. In the first branchial of the Dog-fish the hypobranchial is merely a bud, segmented off from the anterior lobe of the pedate lower end of the arch. In the rest of the principal arches (*h.br* 2, 3, 4) this ventral element is a long terete rod, sharply retral, and forming an acute angle with its fellow of the opposite side: this segment does not exist on the last arch; and its pharyngobranchial is not distinct from that of the fourth branchial (Pl. XXXVII. fig. 2, and Pl. XXXVIII. fig. 2).

The epibranchial and ceratobranchial series are closely like the "epi- and cerato-hyals," save that they are smaller; they are similarly palisaded with branchial rays. In the lower view (Pl. XXXVIII. fig. 1) the seriality of these arches is well seen. The hyoid arch, with its multifid branchial rays, that take the place of the bony opercular and subopercular of the Osseous Fish, is the only arch, besides the last branchial, that

[1] I have figured them in both ways for illustration.

is not supplemented with an "extravisceral" cartilage. There are three pairs of labials in the trabeculo-nasal region—one pair on the pterygo-quadrate arcade, one pair in the mandible itself, and a pair of similar cartilages to each branchial arch save the last.

The first of these external cartilages, which was a small lobe in front of the nasal sac in my third stage (Pl. XXXVI. figs. 3, 4, 5, *l.* 1), and had only one or two slime-glands in it, has now been carried over the great nasal dome behind, and over the basitrabecular in front; it contains a row of about ten slime-glands, and forms the side of the triangular "cutwater."

The second labial (*l.* 2) is a thin lunate shell of cartilage, having an irregularly crenate free margin; it has partly coalesced with the trabecular cornu and anterior rim of the inverted nasal cup; it lessens the size of the nasal opening.

The third labial (*l.* 3) is thick, phalangiform, and twisted; it is applied as a valve to the outer rim of the nasal cup, and exactly corresponds with the "appendix alæ nasi" of the mammal.

The fourth labial (*l.* 4) is a small pointed spatula of cartilage, applied obliquely to the middle part of the outer face of the pterygo-quadrate; its broad end is in front.[1]

The fifth labial (*l.* 5) is very similar, but is smaller, and is applied to the mandible in such a manner as to meet, by its pointed posterior end, the fourth labial; the angle at which they meet is very acute in the closed mouth.

The remainder of the "extravisceral" cartilages may be called "extrabranchiales;" they are four in number, and lie inside the skin of the branchial pouches at the extremity of the branchial rays; thus, in the figures (Pl. XXXVIII. figs. 1 & 2, *e.vs* they are shown opposite the arch next behind. Each bar is sigmoid, pointed above and pedate below. The second has the largest "foot;" the last is rudimentary, and is attached to the fifth branchial, although it belongs to the fourth.

The reason for the absence of an extrabranchial cartilage from the gill-bearing hyoid is not evident; they appear to belong to the same category as the labial cartilages; hence I propose to call them all "extraviscerals."

These extrabranchials are a source of strength to the gill-pouches; they lie in their lower part principally, their pointed end being attached to the free extremities of the branchial rays, between the slits (*clefts*), and close in front of the slit which intervenes between the arch to which that particular extrabranchial belongs and the one next following.

The extrabranchials cease as such in front of the last branchial arch; but they are followed by a pair of precisely similar cartilages, which early coalesce together below by their broad pedate end. These are "extracostal" cartilages; and from them proceed the rays that form the skeleton of the pectoral fins. This pair of coalesced cartilages form the "shoulder-girdle," or scapulo-coracoid belt.

[1] In *Scymnus*, *Squatina*, *Centrophorus*, and others, there is another labial in front of this, which corresponds to the fourth of the Skate.—See Gegenbaur, pls. 11 & 12, and Pl. XLII. fig. 4, *l.* 4, of this paper.

On the Structure and Development of the Skate's Skull.

First Stage: *Embryo of* Raia maculata, $1\frac{1}{3}$ *inch in entire length, seven weeks after deposit of egg*; *and Embryos of* Pristiurus, $\frac{2}{3}$ *and* $\frac{3}{4}$ *of an inch in length.*

The first embryo, taken for me from the egg-pouch of the Spotted Skate in the Brighton Aquarium by Henry Lee, Esq., was, in development, intermediate between the less and more mature embryos of the Dog-fish (from the same friend) already described (Pl. XXXIV.); the two others, the gift of Mr. Balfour, were from the Naples Aquarium. The length of the embryo Rays from Brighton was much greater than those of the Dog-fish, owing to the extreme development of the tail, the anterior part being no bulkier than the smallest embryos of the Dog-fish which I have just described.

The pectoral fins (Pl. XXXV. fig. 1, and Pl. XXXIX. fig. 5) are simple lunate folds on each side of the umbilicus (u); and these embryos, if they had been found detached, could not easily have been distinguished from those of a Shark, the peaked rostrum and the fan-like shape of the fins not being developed as yet.

At present the skeleton of the embryo is quite granular and transparent, so that by careful management most of its structure can be made out without any dissection.

These embryos show, on a good scale, the structure of a vertebrate embryo in its first or simple morphological stage. Many *embryological* processes have been gone through; but now its primordial skeletal parts have been fairly differentiated. The sacs of the special sense-organs are at present horseshoe-shaped folds of the embryonic cuticle and cutis, the large closed brain-vesicles (C^1, C^2, C^3) are full of watery fluid, and the third of these (C^3) is covered very thinly by large soft mother cells. The mouth and pharynx are covered above by the axial structures, and floored below by a continuous throat-skin, above which, behind, is the heart; but the sides are an open grating, hedged in by bowed bars. The mesocephalic flexure is perfect, and the mouth complete. None of the visceral arches meet, right and left; but the pterygo-mandibular bars are coming near each other both in front of and behind the oval mouth. Behind the mouth the visceral bars are yet further and further apart, and the arches themselves gradually lessen in size; above, the hinder arches are set on to the infero-lateral edge of the vertebral structures in the cervical region; half the postoral arches are behind the third cerebral vesicle (Pl. XXXIX. figs. 1, 2, 5, *br*).

Behind the azygous oral cleft the visceral openings are variable in size, the first post-oral cleft (the "spiracle," or "tympano-Eustachian," *cl* 1) is less than the next; it has a pear-shaped outline, and soon fills up below, so that, when developed, this opening, the "spiracle," is seen in the dorsal region, close behind the eye, whilst the others are on the ventral aspect. The second cleft (*cl* 2) is larger, and retains its lower slit-like part. The remainder, between the proper branchial arches, are tolerably even in size, but have less vertical extent behind because of the shortening of the bars. From

all the bars, except the first or spiracle, large, spatulate, external branchial filaments grow[1], six or seven on an average to each bar on each side; they are now, in the longest embryo, the largest of them, as long as the head; each contains, as in the embryo of the Dog-fish, a single capillary loop. Four short buds appear in the "spiracle," or first postoral cleft (Pl. XXXV. fig. 1, *cl* 1): in embryos that are evident *Skates* a large pseudo-branchia is seen inside the front wall of the spiracle, and arising from the back of the proper apex of the mandible (Pl. XL. fig. 3, *cl* 1, *ps.br*).

The branchials (*br* 1–5) are simple rods; not so the rudimentary mandibular and hyoid arches; these are bifoliate above, more markedly *bifurcate* than in the Dog-fish, in which they were pedate (Pl. XXXIV.).

Here the bifurcations are filled with granular substance, which becomes solid cartilage in each fork; and in this the Skate comes nearer to the ganoid and teleostean fishes.

In each case the hinder spur is slenderer than the front; and in the mandibular arch it is seen that the hinder hooked snag is but loosely connected with the main part. This is in front of the "spiracle" (*cl* 1); but, behind this opening, the front part of the next bar is severed from the long hinder stalk.

The front fork of the mandibular arch turns downwards and forwards to become the upper jaw; the small backwardly curved spike, the hinder fork, becomes the spiracular cartilage.

In the second arch (hyoid) the large front fork becomes the hyo-mandibular, and the rest of the bar the proper hyoid. A reference to the figures will show that the suspensorium of the mandible, the hinder fork, although it embraces the anterior spiracular lip, is yet attached to the head below and behind the exit of the trigeminal nerve, antero-inferiorly to the auditory sac; it is a *free* "otic process."

The anterior fork of the hyoid arch is in inferior relation to the auditory sac; it articulates broadly with it afterwards as the hyo-mandibular, whilst the hinder fork, or "stylo-ceratohyal," is loosely connected with that sac behind. In the various types, and even in the various stages of one and the same type, the hinder division of the second postoral is very variously articulated to the surrounding parts.

It is worthy of remark that that which distinguishes the Rays from the Sharks most completely, namely the mode of segmentation of the hyoid arch, is already evident in the embryos at this stage. The Skate breaks up this arch in the same manner as the Sauropsida and the Mammalia; whilst the Shark shows it in a simple and low form. I have worked out the basis cranii in the youngest *Pristiurus*, $\frac{2}{3}$ of an inch long, and the visceral arches in the larger specimen of *Pristiurus*, $\frac{3}{4}$ of an inch long (Pl. XXXV. figs. 3 & 4).

When the base of the skull is seen from above (fig. 3) there are three *intercapsular* regions displayed, although the bend of the head throws the eye-ball into the same vertical line as the nasal sac (see fig. 1). If we suppose a curved line passing con-

[1] They are small in the first cleft.

tinuously through the middle of the sense-capsules in the first figure, that will represent the edge of the preparation figured in fig. 3. Such a line would bend strongly downwards (at about 120°) in front of the ear; and that is where the middle and hinder regions meet; these are the trabecular and parachordal tracts.

The parachordal tracts (*i v*), or investing mass, are cut away, as it were, to fit to the convex edge of the ear-capsule; and being bevelled, they pass under each sac somewhat. They then broaden, where the postaural nerves (9, 10) pass out, and then, narrowing a little again, are equal parallel bands, running without transverse segmentation some distance into the cervical region; and the numerous roots of the vagus and the following spinal nerves are seen at their outer edge (fig. 3. 10, *sp.n*).

In front the parachordals thin out a little, and pass under the ends of the next pair of bands—the trabeculæ; these are wider, shorter, and more solid tracts of crowded cells, taking up the carmine more perfectly, and rapidly becoming hyaline cartilage.

They form afterwards the flattest of skulls; and now are wide flat bands, angular behind, where they are wedged in between the parachordals and the ear-sac; they then narrow at their waist, and broaden into a rounded spatula in front, close behind the olfactory capsules.

They are not merely *præchordal tracts*; for the notochord reaches to their middle (Pl. XXXV. fig. 3, Pl. XL. fig. 7, *tr*, *nc*), where it is twisted, recurved, and constricted in a moniliform manner, like the floral hairs of *Tradescantia virginica*. The rest of the notochord is unconstricted, and passes, of an even size, into the uncleft spinal region. The pituitary space is just equal in size to the notochordal tract of the trabeculæ; it is oval, and is only finished in front by a newer and softer tract of tissue—the rudimentary internasal band. The infundibulum passes obliquely into the pituitary sac (*inf*, *py*), the latter getting somewhat under the apex of the notochord.

Behind, the posterior clinoid edge of the trabeculæ runs inwards and forwards and externally; the trabeculæ then widen to their "elbow" or most projecting postero-external point. In the angle between this point and the fore margin of the ear-sac, the præauditory nerves (5, 7) are seen as large leashes of young fibres in four main divisions, the fourth (facial nerve, 7) hooking round the front of the capsule. Antero-internally to that capsule a mass of cells can be seen, the rudiment of the Gasserian ganglion, and postero-internally another smaller mass, the rudiment of the ganglion of the ninth and tenth nerves. The oval olfactory sacs (*na*) have between them a dagger-like internasal tract, which, like the covering of those sacs, is very soft at present; this is the rudiment of the internasal part of the trabeculæ, the cornua, and the prænasal rostrum (*i.nc*).

The pointed end of this tract now lies *behind the mid brain*, truly a remarkable position for the rudiment of that long beak which afterwards forms the axis of the "cut-water" of the Skate, and even of the Saw-fish, whose structure corresponds to that of the Skate (Gegenbaur, pl. 14. fig. 2).

In an embryo of *Pristiurus* $\frac{1}{12}$ of an inch longer than the last ($\frac{3}{4}$ of an inch), all the *postnasal* structures of the skull-base were clean removed, and the upper wall of the fauces and the pharynx shown (Pl. XXXV. fig. 4).

The parts last described are shown *in situ*, as in fig. 3 ; and the whole series of post-oral visceral arches are shown : they were seen as a transparent object, and the preparation flattened a little. The pith of the facial rods took the carmine well, and had become true hyaline cartilage. If this figure be compared with the side and lower views of the younger embryo, drawn in its undissected condition (figs. 1, 2), the following description will be easily understood :—

The first cleft or spiracle (*cl* 1) is wide at the top and a mere chink below ; its direction during the mesocephalic bend is backwards and downwards, its opercular lip, or "vallance," looking upwards, and, from lack of breadth, exposing the *four short external* branchial filaments. Within this opercular fold an oval cartilage is found (fig. 4, *sp.c*) ; this is the "spiracular cartilage," and corresponds to the apex of the mandibular bar of an embryo Salmon ("Salmon's Skull," pl. 1. fig. 7, *mn*). Compared with the Urodele or Batrachian, this rudiment must be considered to correspond to the "otic process," and not to the "pedicle" (Huxley, 4, p. 42)[1]. On each side, below this spiracle, its operculum and its contained cartilage, the wall of the mouth (*m*) is thick, and strongly bent upon itself ; this thick part extends from the chin behind to the front of the mouth and the nasal sacs. Each lateral cartilage is a thick *half-link*. Were the two confluent at the mid line, they would make a transversely placed link or oval ring ; but they lie askant, the forebent part being higher than the part behind the mouth. The fore part is flatter, and the hind part thicker than the rest ; but they both are widened at the end, and turn, in a pedate manner, outwards. Behind their middle the cartilage is becoming somewhat loose in texture ; a transverse cleft has begun in its substance ; and this evident break in the cell mass has its concave margin looking forwards.

Behind this line we have the rudiment of the lower jaw, in front of it the upper ; and the latter will have a convex end, to fit into the concavity of the former. The upper jaw is called the "pterygo-quadrate" bar ; for the quadrate region has its apex independently developed, and the large foregrowth of the bar is built into the whole side of the palatal ceiling. The mouth, thus encircled and fringed in front by the slightly bilobate fronto-nasal process (fig. 2, *f.n.p*), is ear-shaped, a long transverse oval with a short anterior expansion.

Considered as the *first branchial arch*, which in reality it is, we thus have an independently developed upper segment and a commencing division of the main bar into an "epibranchial" piece, which grows forwards and inwards, and a "ceratobranchial," which grows downwards and inwards.

The next arch is similar to the last ; it is the hyoid, and also has an oval cartilage above, and a long bar lower down, also strongly bent upon itself.

[1] See also the adult Skate's skull (Pl. XLI. fig. 4, *mt.py*).

A difference is to be noted at once; for the spiracular cartilage is developed in the *posterior fork* of the first visceral arch, and this nucleus in the *anterior fork* (Pl. XXXV. figs. 1 & 4).

The mandibular nucleus looks outwards and backwards (*sp.c*); but this is turned directly forwards at right angles to the main bar (fig. 4, *h.m*, *hy*. Compare also here the adult skull, Pl. XLI. fig. 4, *mtpg*, *hm*); the "metapterygoid" is the same as the spiracular cartilage *in the Skate*).

The main hyoid bar is a slender tape of cartilage, pointed finely at each end, and far from the mid line at both ends; it is undivided at present.

The next *five* arches are the ordinary branchials: the first is much larger than the hyoid; and then they gradually lessen, the last being very small.

These arches are strongly bent upon themselves, the pharynx of the embryo Skate being a depressed pouch with extensive lateral fissûres or clefts (figs. 1, 2 & 4).

The main part of each arch is pointed above, the point looking slightly forwards, and blunt below, this rounded lobe looking backwards; both ends come much nearer to the mid line than in the hyoid arch. In the roof of the pharynx, where the front clefts close, there is, just above each main branchial, an independently chondrified piece—the "pharyngo-branchial" (*p.br*); each piece is lunate, pointed outside, blunt within, and having its point turned more backwards than outwards, although their general direction is transverse.

These free cartilages cannot very safely be considered as the serial homologues of those above the two first arches; they are not at the side of the face, but right beneath the edges of the parachordals, where the leashes of nerves are given off (figs. 3 & 4).

A separate cartilage, developed at the end of the pterygo-quadrate, or one above the point of the main hyoid, would correspond more truly.

The further segmentation and metamorphosis of the skull and its arches will now be described. I have shown above what, from the beginning, was independently chondrified, and now will show how the main bars break up.

Second Stage: *Embryo of* Raia maculata, 4 *inches long*; *body* $1\frac{1}{3}$ *in.*, *tail* $2\frac{2}{3}$ *in.*; *time from deposit of egg-pouch* 3 *months.*

This important specimen was taken for me from the Brighton tank by the same valued friend, Mr. H. Lee; and although the time of its growth was less than twice that of the early specimen, the development and metamorphosis was quite perfect—that is, as to chondrification and segmentation.

There is much that is instructive to the morphologist in the external characters of this embryo (Pl. XL. figs. 1 & 2, drawn as far as to the umbilicus, *u*). In front the beak has become fixed to the anterior angle of the outspread, gigantic, flabelliform pectoral fin (*p.f*), which is seen curling round the depressed cheek. Above, the beak is seen to be separated by a deep crescentic sulcus from the rounded cranial sac; and

the flattened eye-balls are carefully lodged in sockets, the inner half of which is formed by the semicircular superorbital cartilages, the horns of which are grafted on to the nasal sac in front and to the auditory sac behind. Outside the posterior horn of the superorbital (sphenotic process) is the first postoral cleft, or spiracle (Pl. XL. figs. 2 & 3, *cl* 1); its narrow inferior part has been filled in, and only the upper expanded end has kept open—widely open, however, and showing on the spiracular or metapterygoid cartilage a comb-like "pseudo-branchia" (*ps.br*), composed of about eight branchial papillæ. Behind the spiracle the gill-bearing hyoid and the proper branchial arches are seen elegantly spreading into a U-shaped system of pouches, growing, as it were from a massive stalk, the occiput and spine.

Below, behind the basitrabecular beak, the fronto-nasal process (*n.f.p*) is very large and persistent, forming a free, anterior, emarginate lip, with the valvular nasal openings (*na*) in their primordial ventral position, with enclosed "labials" to guard the openings.

The angles of the mouth are lipped at right angles to the transverse inferior oral opening; but the mandible has its gums and teeth quite bare. The angulo-labial fold is continued backwards as part of the general *opercular* skin, which further backwards and outwards is imperfect in five places on each side. These places are the branchial clefts; they are the retained lower ends of the huge primary clefts. The general opercular fold which has covered the open grating to so large an extent is seen to develop a special ear-shaped flap to each of the branchial outlets.

Embryos as large as this, when carefully examined, have protruding from their branchial clefts what might, at first sight, be mistaken for a parasitic growth of filamentous confervæ. These, however, are the still retained external branchiæ. They have begun to shorten in the first opening; but most of them are very long (Pl. XL. fig. 1, *e.br*). They are spatulate at their free ends; and their single vascular loop is still functional.

Between and behind the branchial apparatus is the large, short umbilicus (*u*), which connects the embryo with a yolk the size of a dove's egg.

The chondrocranium, with its appended basketwork of visceral arches, is now complete, both as to chondrification and segmentation.

On the whole very similar to that of the Shark at the same stage (Pl. XXXVI. figs. 3, 4, 5, and Pl. XL. figs. 4, 5, 6), it yet differs in several important points.

The cranium seen from below (Pl. XL. fig. 6), with the eye-balls removed, is seen to be composed of four pairs of primary elements. Behind, the "parachordal" cartilages that invest the notochord (*i v*, *nc*) have coalesced with the hinder pair of "paraneural" capsules, those of the ear. This four-sided shorter hind part of the basis cranii has coalesced in front with another pair of outspread cartilages—the trabeculæ (*tr*); and these, also, in front have coalesced with the foremost paraneurals—those of the nose (*na*). Where the four basal plates meet, the internal carotid arteries (*i.c*) enter; and in front of these is the appearance of a space and a slit, not so densely chondrified:

these are marks of the primary pituitary space (*py*), the soft tract between the bowed edges of the trabeculæ. The trabeculæ have developed a common basal piece, the "basitrabecular" rostrum (*b.tr*); but this is not segmented off as a distinct bar. Where the trabeculæ have so completely coalesced in front, forming also their basal rostrum, they turn upwards into the frontal wall of the face, and finish the cranial floor. The nasal sacs are hollow inverted cups of cartilage, with their downturned mouth stopped largely by "labials." The rim of the cup is strong on the outside, and also gives attachment to an ethmo-palatine cartilage (*a.o*).

The roof, also, of the nasal sac is modified in its form by reason of the engrafting upon it of a large bowed cartilage, the "superorbital" (fig. 4, *s.ob*), a cartilage which has but little independence of growth, but the substance of which early appears in the embryo. The lower edge of this cartilage, mesiad of the eye-ball, is continuous with the trabecular crest; and the "tegmen cranii" grows directly from it towards the mid line of the roof. The roof and side walls are *analogous* to the upper portion of a vertebral arch.

Here, however, in the Skate, the tegmen is largely undeveloped; the brain-sac is permanently membranous above in front, and rests upon the laminar trabeculæ. Then, just in front of the nasal region, there is a cartilaginous beam thrown over; but it is narrow, and thence to the ear-sacs the roof is bare of cartilage. Behind, the tegmen reappears, and helps the superoccipital to roof in the hinder brain between the auditory masses (*au*). The superorbital arc grafts itself also on these sacs; hence the *compound* region, which ossifies separately in the "Teleostei," behind the orbit, the so-called postfrontal or sphenotic.

The clear but cheese-like cartilage shows the three canals through its walls (*a.s.c*, *h.s.c*, *p.s.c*); and where the anterior and posterior of these unite, the "aquæductus vestibuli" is seen open.

Behind, a mass of notochord is still to be seen, and the parachordal cartilages project backwards outside, to form the occipital condyles (*oc.c*). The epiotic elevation over the junction of the anterior and posterior canals is slight; the pterotic ridge outside the horizontal canal is well developed.

The oral and pharyngeal visceral arches (the first or trabecular has been described as part of the chondrocranium) are nowhere more instructively developed than in the Rays.

Keeping the eye upon the early condition of these parts (Pls. XXXV. and XXXIX.), we shall see what metamorphic results have been brought about.

The apex of the first postoral or mandibular arch has been developed as a distinct crescentic cartilage, the "spiracular cartilage" or metapterygoid (Pl. XL. fig. 4, *mt.pg*); it is attached below the sphenotic process, and behind the fifth nerve; it is the bearer of the "pseudo-branchia" (*ps.br*), lies in the anterior wall of the first cleft, and answers to the "otic process" of an Amphibian. This detached suspensorium is joined to the quadrate region by a ligament; it answers to the hinder fork of the visceral rod. The larger anterior fork, the posterior extremity of which is part of the main descending bar

(the quadrate, *q*), has grown forwards, and has become a large upper jaw, the "pterygo-quadrate;" whilst the remainder of the primary stem hinges with the outturned end of this as the lower jaw—articulo-Meckelian (Pl. XL. figs. 4 & 5, *q.pg*, *ar.mn*).

These two arches (*two* by metamorphosis) in rest are but slightly bowed forwards, where they meet their fellow bars of the opposite side; they are almost directly transverse, and conform, as every thing else does, to the flat outspread form of this peculiar type of Fish.

The second postoral (hyoid) was also forked above in the early embryo; the further development of that arch is similar to what takes place in the Teleostean (*e.g.* Salmon); but it is arrested at a lower morphological level.

The anterior fork of the second postoral articulates with the auditory capsule beneath the pterotic ridge ("tegmen tympani") by an oblong condyle above (Pl. XL. fig. 4, *h.m*), whilst below it becomes detached entirely from the rest of the bar, turns forwards close behind the spiracle, which it protects, as the metapterygoid does in front, and then fastens itself strongly by ligamentous fibres to the quadrate, becoming its new additional suspensorium.

The hinder fork, or proper apex, is wholly freed from the hyo-mandibular; its upper piece, or "epihyal," is in reality only *half* the epihyal region, having lost the hyo-mandibular wedge. Thus the expanded apex of the arch is cleft obliquely, as in Sauropsida and Mammalia, and not from top to bottom, as in Teleostei, nor simply across without subdivision of the "epihyal" region, as we have just seen in the Dog-fish. The bar, freed from the anterior fork, is now developed into a rather feeble branchial arch; it is attached by ligament to the end of the jutting pterotic above; and the upper or epihyal segment is exactly like the epibranchials (Pl. XL. fig. 4, *e.hy*, *e.br*), save that it is smaller than most of them, and, being attached to the corner of the skull, sends no "pharyngo-pleural" segment over the pharynx. There is no *secondary* cartilage developed in the attaching ligament, as in Teleostei; the "interhyal" ("stylohyal," Cuv.) is fibrous.

The ceratohyal (*c.hy*) is feeble, but normally branchial in character; the arch is finished below by a small styliform hypohyal segment; this is attached by ligament to the first hypobranchial (fig. 5, *h.hy*, *h.br* 1).

Here we see a vast difference between the Shark and Skate; for in the former the stout two-membered bars of the hyoid have their ventral ends strongly articulated to a large basihyal piece; whereas in the Skate the lower ends of the hyoid are nearly as far apart as the breadth of the transverse mouth.

The five branchial arches (*br* 1–5) are very uniform, only decreasing gently in size from before backwards. Each is composed of a superpharyngeal, apical piece, the pharyngo-branchial, an epibranchial, a ceratobranchial, and a hypobranchial on each side (*p.br*, *e.br*, *c.br*, *h.br*). These arches are strongly bowed outwards, and bent on themselves; their lateral parts are thick, and grooved externally. A single series of cartilaginous

branchial rays proceeds from each; these are pedate at their outer ends. The ventral segment (hypobranchial) is more or less adze-shaped (fig. 5, *h.br*); but this obtains only in the second to the fourth. The first has this segment very long, at first dilated, and then very slender, and the right and left are early fused together. The last branchial arch has its pharyngo-branchial united to that of the fourth, and its hypobranchials (*h.br.* 5) completely united. These fused elements look like an azygous piece; but in the adult of *R. clavata* (Pl. XLII. fig. 4, *h.br* 5) they are very partially united, and, as to form, are seen to be only a modification of the adze-shaped or fan-shaped type.

At this stage the branchial arches, including the hyoid, carry two sets of branchiæ in full function. The *external* are at their highest development; and the internal plates are perfect, although small.

The "extrabranchials" are absent, as far as I can make out, in different kinds of Skates[1] (*R. clavata*, *R. maculata*, &c.); nor is there a labial on the mandible. But there are four pairs of præoral labials—three acting as nasal valves (*l* 2, 3, 4), and the pair (*l* 1) attached to the side of the "rostrum," but not riding upon the nasal sac, as in the Dog-fish.

Third Stage: *Embryos of the Thornback Skate* (Raia clavata) *nearly ready for exclusion from the egg-pouch.*

In the last stage the metamorphosis was complete; this third stage is given for the sake of the vertical and transverse sections, which reveal the architecture of this kind of chondrocranium. A longitudinally vertical section with the brain removed (Pl. XLI. fig. 1) shows a hollow barge-like structure, with a cartilaginous bottom perfect, and projecting as a free prow—the basitrabecular rostrum (*b.tr*)—whilst the "deck" is only cartilaginous fore and aft over the ethmoidal and the auditory region. The various nerve-outlets (1, 2, 5, 7, 8, 9, 10) are easily recognized. This little boat is undergirded by transverse bars that appear in the section—the pterygoid, mandibular, and first and fifth hypobranchials (*q.pg*, *mn*, *h.br* 1, *h.br* 5).

The first transverse section shows the nasal caps or domes (*ol*) far apart; these are connected by a large bridge of cartilage, convex below and concave above. Thus there is formed a large præcranial space; for the frontal skin is convex.

An *inner* labial (*l* 2) is seen in section; the palatal skin follows the convexity of the cartilaginous bridge; that bridge is formed by the trabeculæ and their commissure (*tr.cm*). Here are the very elements of the nasal septum and roof of the higher types; but the trabeculæ have only united below; they are far apart; and their crest applies itself normally to the inner edge of the nasal dome, yet forms a structure widely different from that which obtains when these domes are closely adpressed, and the trabecular

[1] In the Torpedo the dilated ends of the branchial rays unite outside the pouches in such a manner as to form a practical "extrabranchial" band (Gegenbaur, pl. 13. fig. 3, pl. 20. fig. 1).

crests close together, ready for fusion at the mid line: the *distinct* antorbital (*a.o*) is cut through. In an *antorbital* section (Pl. XLII. fig. 1), the nasal dome is seen to be thickened by the superaddition of the engrafted superorbital arc; and, in this its hinder part, the nasal sac is some distance from the trabeculæ and the cranial cavity. The trabecular crest has also received increment from the same "brow" of cartilage (*s.ob*); and thus the *deck* is partly covered in—entirely for a short distance, a little further back. Beneath, the pterygoid undergirders are seen, where they join by a fibrous band.

A section (Pl. XLII. fig. 2) behind the mouth (*m*) and through the eye-ball (*e*) shows the squared form of this little barge, also that the brain at the time of hatching well fills its cavity. The upper third of the "orbito-sphenoidal" side wall is due to the thick brow-cartilage (*s.ob*), the rest to the trabecular crest; the floor, thicker at this part, is a trabecular commissure.

The quadrate part of the upper jaw is here cut through, and also the whole extent of the articulo-Meckelian bar, with its distinct symphysis, its projecting angle, and its cupped articular surface for the rounded quadrate condyle. The mouth (*m*) is shown as in a nearly closed state; it has much mobility, because of its free *double* suspensorium, its well wrought articulo-quadrate hinge, and its anterior and posterior fibrous symphyses at the ventral extremities of the two arches.

The last section (fig. 3) to be described is through the auditory sacs, somewhat obliquely, near their posterior wall; for it can be seen that the occipital arch is here complete, crowned with a veritable spinous process, having neurapophysial sides that form a gothic arch, and a broad base, on which lies the diminished and fading cephalic notochord.

On the right side the horizontal canal (*h.sc*) is cut through where it overarches the condyle for the hyomandibular (*hm*). On the other side, the posterior canal is cut through, the razor cutting further back; and the "interhyal" ligament is seen carrying the epihyal (*e.hy*) with its three branchial rays, below which part of the ceratohyal (*c.hy*) is seen, with three more rays. On the right side, under the hyomandibular, most of the ceratohyal is seen (*c.hy*) with its flat rays, and below it the little hypohyal (*h.hy*) attached to the long slender hypobranchial belt of the first proper branchial arch.

This figure shows the breadth of the pharynx whilst in a state of rest.

Fourth Stage: *Skull of adult Thornback Skate* (Raia clavata).

The skull of the adult Skate may be said to be fiddle-shaped (Pls. XLI. and XLII.); for it has very pinched sides, is very flat, and has a long stem or handle. The narrowing of its body is to make room for the eye-balls; the bulging parts are the auditory sacs behind, and the wider nasal sacs in front; and the projecting shaft is the enormously developed basitrabecular rostrum, which in this and related types acquires its uttermost development.

The interauditory part only of the base of this chondrocranium is formed by the "parachordal" cartilages; from the postpituitary wall to the end of the snout all the

rest is trabecular. On the upper surface it is easy to see how much building-material has been used to form the superorbital arcs; whatever their morphological nature may be, they are parts that do not chondrify separately, but are very distinct in early embryos, as I have shown in my paper on the Salmon. Behind, the crested form of the auditory masses is seen to be largely due to the form of the great loops into which the internal sac is developed: the primary opening, or vestibular "aqueduct" (*aq.v.*) is only covered by skin. The interorbital space above is still retained as a large oblong fontanelle; then there is a short and narrow bridge of cartilage, and then, in front of that, the lanceolate opening into the great præcranial or internasal vacuity. On each side of this gaping space the trabeculæ, as they melt into the rostrum, grow over as an internasal eave. These ascending and upper growths of the trabeculæ represent, by a sort of morphological hypertrophy, the trabecular crests of a bird or mammal that form the lower portion of the mesethmoid. The nasal sacs, very large and wide apart, are modified from their original dome-shape by the condyle on their outside for the rib-shaped antorbital (*a.o*), and by the addition of a new stratum of cartilage yielded by the great superorbital arc. The same arc still shows its form behind, where it has thickened the periotic mass, and formed the sphenotic process (*sp.o*). Between the superorbitals the skull is flat above; and below, the basis cranii is only very gently convex.

The occipital condyles (*oc.c*) project but little; and a tract of notochordal jelly is interposed between the median part and the first vertebra. The nerve-outlets are most of them best seen in the side view (Pl. XLI. fig. 4. 2, 5, 7). The peculiar mode of suspension of the double dentigerous arch is best seen in the side view (Pl. XLI. fig. 4, *q.pq*, *mn*, *mt.pg*, *hm*); the hyomandibular running forwards to the base of the metapterygoid, or spiracular cartilage, to be attached by ligament to both the quadrate and the angle of the mandible. The loose spiracular cartilage bears but little of the weight of the jaw; of which it is the proper apex.

In the lateral view the arches are compressed as much as possible for display; in the upper and lower views they are in a state of rest, and therefore greatly depressed.

The pterygo-quadrate bar is attached in front by ligament behind the nasal sac; and the ligamentous fibres attached to the round inferior end of the oblique subtrihedral hyomandibular spread fan-like, to insert themselves on the top of the quadrate and the angle of the mandible. The latter is hinged in a somewhat complex manner, a ball on the quadrate slipping into an articular cup, which has three nodules on its rim, whilst the whole mass of the angular region is thin-edged.

The articular part of the upper bar—the quadrate—is separated by a cleanly made *neck* from the proper pterygoid region; but no inspection of the parts in the adult would have led to the discovery of the fact that this upper dentigerous bar, in its toothed part, is a mere process or fork of the mandibular or first postoral bar. The posterior part of the hyoid is seen to be jointed by its epihyal part (*e.hy*) to the end of the condyle of the hyomandibular; the ligament is almost the length of the so-called

" stylohyal " (" interhyal ") of the Teleostei; but it has stopped in its metamorphosis at that point where, in the osseous fish, there are *two* subequal hyoid arches (" Salmon's Skull," Third Stage, pl. 2. figs. 6 & 7, *hm*, *c.h*). In the Teleostean the ligament would be more than halfway down the side of the hyomandibular (*three fourths* in the Salmon, ibid. pl. 6. figs. 1, 2 (*hm*, *st.h*). Also in the osseous fish, a nodule of cartilage appears in the ligament, like a rudimentary *meniscus*, which grows into a terete rod and ossifies (ibid. *st.h*).

The small epihyal (*e.hy*) is not only attached by its apex to the hyomandibular, but also it is closely tied to the front of the first epibranchial at its upper third; this gill-bearing bar is succeeded below by a ceratohyal of equal size (*c.hy*); and then there is below it a small styloid hypohyal (*h.hy*), situated on the notched proximal end of the first hypobranchial (*h.br* 1).

At first sight it would seem as though the hyoid had formed a commisural band across behind the mandible (Pl. XLI. fig. 4, *h.br* 1); but that is the belt formed by the fusion of the first hypobranchials. The normal direction of the pharyngo-branchials (*p.br*) is backward; that of the fourth is continuous with the epihyal of the fifth, as there is no separate pharyngo-branchial in the last arch.

The epi- and ceratobranchials are tolerably stout, flat within, grooved outside, and strongly tied together by fibrous bands. The arches end below in flat, kidney-shaped, adze-shaped, and even flabelliform hypobranchials (*h.br*). That of the last coalesces in some degree with its fellow; and the notched and split plate thus formed reaches by its fore horns nearly to the hypobranchial girder of the first arch.

About twelve or thirteen branchial rays are attached to the hinder edge of each arch (see Pl. XLI. fig. 5, *br.r*, for those on the hyoid). These are pedate at their distal ends, which lie in the outer wall of the sac; and in some of the larger Skates their extremities are very large and lobate.

It is impossible, in the Skate, to prove that the whole of the trabecular growth is not axial. Attached to the nasal sac of each side is a large, solid, short, rib-like antorbital (*a.o*), evidently a præoral visceral bar.

The " labials " are the only " extravisceral " found by me in this type. There are four on each side; and the fourth is but slightly connected with the pterygo-quadrate bar (Pl. XLII. fig. 4, *l*. 4).

The first pair (*l*. 1) are lanceolate and notched in front; they help the " cutwater " or " rostrum " very little, being carried away far from the nasal sacs, on which they are mounted behind in the Shark (Pl. XXXVII. fig. 2, *l* 1). The second labial (*l* 2) is in front of the nasal opening; the third (*l* 3) outside; the fourth[1] (*l* 4) is articulated to the second, and lies inside *below* the rim of the cup and the fore edge of the pterygoid bar.

[1] This fourth labial of the Skate does not answer to the fourth of the Dog-fish, but to the *inner* of the two on the pterygo-quadrate of *Scymnus, Squatina*, and *Centrophorus* (Gegenbaur, pls. 11 & 12, *L*: the next is marked *L'*.

These thin valvular cartilages are of great interest to the morphologist: the second and fourth are exactly repeated in the Snake tribe; the fourth is often large in birds (e. g. *Rhea*, *Turnix*, some "Picidæ," and the "Passerinæ" generally). The fifth, or mandibular labial, which is absent in the Skate, but present in the Shark, I found thirty-five years ago in the Coot, and later in the Gallinule.

The third labial (*l* 3) has only to be compared with the "appendix alæ nasi" of an embryo mammal for the two to be immediately recognized as representing each other.

Summary and Conclusion.

The skull of the Selachians may be expected to yield much instruction to the morphologist. I shall compare the varieties of it seen in that great group with each other, and then with the skull of various other types.

A. *The skulls of the Dog-fish and the Skate as compared with each other and with what is seen in the Selachians generally.*

The Dog-fish and the Skate are representatives of the two main divisions of the Elasmobranchii, and are fairly typical of the two suborders.

In their outer form the Sharks differ but little from that of an embryo Teleostean at about the time of hatching; the Skates mask this form by their extreme flatness and the huge expanse of their outspread pectoral fins. Their embryos differ but little in outward appearance, as Mr. Balfour's figures (Q, pl. 25) and mine clearly show; but as soon as the skeletal elements can be traced their divergent development can be seen.

Besides the long external branchials of the hyoid and branchial arches, each type shows *four* free external branchiæ emerging from the spiracle; and the *papillæ* actually developed are twice that number.

The postoral arches are, normally, seven; but there are *eight* in *Hexanchus* and *nine* in *Heptanchus*.

One important difference has been shown in this, namely that the postoral "extra-viscerals," which are so well developed in the Dog-fish, do not appear in the Skate.

Another contrast lies in this, namely that the hyoid rays are more or less split or digitate in the Sharks and undivided in the Skates.

As a rule, the cartilage developed in the spiracular operculum in the Shark (it is small in *Scyllium canicula*) is a ray (or rays); in the Skate it is part of the *body* of the arch. There is *one* ray in *Squatina*, *Mustelus*, and *Galeus*; *two* in *Scymnus*, and *three* in *Centrophorus* (Gegenbaur, pls. 11 & 12).

In the Torpedo (ibid. pl. 13. fig. 3, *kr. a.b*) there are *three* small subsidiary cartilages besides the main "metapterygoid" segment in front of the *spiracle*. In *Cestracion* (Huxley, 4, p. 42, fig. 8, *ot.p*) the spiracular cartilage is a free "otic process," or metapterygoid. The transverse position of the mouth, which is so perfect in the Skates, is much more oblique and projecting in the Sharks, and is more like what is seen in

other fishes in that respect; in *Hexanchus* and *Heptanchus* (Gegenbaur, pl. 10) the mouth is very Batrachian.

The upper fontanelle is more completely closed in Sharks than in Skates, although some of them have a nearly perfect "tegmen" (ibid. pls. 7, 8, and 13).

The "cutwater," or facial rostrum, is least developed in the Sharks, and attains its highest development in Skates, especially in *Pristis*.

In Sharks the nasal domes approximate in the adult; in Skates they are permanently far apart (ibid. pls. 7, 8, 13, 14).

The "aqueduct" leading to the ear-labyrinth is seen in the roof of the skull in both types; and they agree in a large number of characters, as the double occipital condyles, &c. But their points of nonconformity are of the highest interest, and this especially in regard to the "visceral arches."

The structure of this group seemed to me for some time to be most conclusive against the theory of the independence of a palatine arch in front of the mouth, as the pterygo-quadrate arcade is in them manifestly the foreturned upper region of the mandibular arch, or a huge outgrowth or process from that arch.

But much comparative study of the Selachian skull and that of the Amphibians has shown me that I had been missing the true "ethmo-palatine" element, a very distinct thing from the pedate process of the quadrate or mandibular pier.

In some Sharks, and in all the Rays, a rib-like cartilage grows in front of the eye on each side, either attached to the nasal dome itself or to the lateral ethmoidal region. In many of the Sharks it is exogenous, and does not exist in the form of a separate cartilage; but it is much more clearly seen in the embryo than in the adult (Pl. XXXVII. figs. 1 & 3, *a.o*).

It is most distinct in *Heptanchus*, and is very definite in *Hexanchus* (Gegenbaur, pl. 1. figs. 1 & 2, M). The *process* can be seen in *Acanthias* (ibid. pl. 2. fig. 3, M′); but all Gegenbaur's figures show in the Rays what I have found in *Raia maculata* and *clavata*—namely, a large antorbital or ethmo-palatine cartilage, whose title to be called a rudimentary visceral arch I shall discuss anon.

The trabeculæ, up to, or even *between* the nasal sacs, must be considered to be *cranial* and not *facial*; yet in front they send out three facial "processes," that in an exogenous manner represent visceral arches.

Thus it appears to me that there are *visceral* rudiments in the face both before and behind the nasal capsules. That these arrested *arch-piers* derive their nervous supply from the huge crowded nerves that also freely grow down into the postoral region, cannot surely tell against their ventral or visceral character; they are aborted or arrested *piers*, and have no free inferior arch, like the mandible and the hyoid cornua.

The sharpest contrast between the Shark's and the Skate's facial basketwork is seen in the manner in which the hyoid arch becomes segmented and specialized.

In *Scyllium canicula*, as we have just seen, both the *primary* mandibular and hyoid

arches are bent forwards above, and they both simply become segmented at the bowed part into an epi- and ceratopleural element.

In the first arch the epipleural element is the pterygo-quadrate, and the ceratopleural the free mandible; in the hyoid the epipleural is the hyomandibular, and the ceratopleural the free hyoid cornu (Pl. XXXIV. fig. 1, Pl. XXXVIII. fig. 2).

This is a very simple piece of morphology; and if the modification of these arches had stopped here their meaning would have been evident.

But in the Skate we have at once a hyoid arch as difficult of interpretation as that seen in so many *higher* types of Ichthyopsida, and of the air-breathing Vertebrata generally; so that the first, as it were, of a whole series of puzzles is set before us.

In the Shark the first and second arches are merely "branchials," without distinct pharyngo- or hypopleural elements.

In the Skate the hyoid arch abutting above against the skull does not grow over the pharyngeal roof, as in the succeeding arches (Pl. XXXV. fig. 4, *hm*, *hy*), and has therefore no pharyngo-pleural element.

But in the forked expansion formed by the primary bar, cartilage commences in two places—a little nucleus in the front fork, and the apex of the main bar in the hind fork: thus the cartilage of the epipleural region is primarily double. A similar puzzle offers itself in the first arch; but the order is inverted: in it the hind fork has its own little nodule of cartilage, and the main bar runs in the front fork; thus the epipleural region of the mandible has two sources of cartilage—a small hinder part, and a large (the main) front part.

In the Dog-fish the two hyoid elements get close within the articular region of the mandible, and are strongly strapped to it by a hyo-suspensorial or *symplectic*, and a mandibulo-hyal ligament.

In the Skate the little front cartilage of the hyoid arch becomes the large hyomandibular, being loosely connected with the rest of its own arch, and having the whole mandibular apparatus suspended to its distal end, so that the mandibular arch is "hyostylic," as in the Shark; yet it is not only suspended on the upper element, but has also a feeble metapterygoid or *otic* suspension; it is somewhat "amphistylic."

B. *The Skull of the Dog-fish and Skate, as compared with that of the more generalized Selachians, of the Chimæroids, of the Dipnoi, and of the Amphibia.*

All these types may profitably be compared together; much, however, of this work I find admirably done to my hand, in Professor Huxley's paper on *Ceratodus* (P. Z. S. Jan. 4, 1876 [1]).

[1] The harmony between the author of that paper and the writer of this is almost perfect. One *little* and one *great* difference of opinion exist: namely, his "angulare" in *Ceratodus* and the Amphibia is my "articulare," p. 34; and the second, or great difference, is the relegation of the trabeculæ by him to the "pleural" elements (p. 32). I have shown in the present paper my own change of opinion, and now consider them to be *pro-parachordal tracts*, ending in exogenous "pleurals."

With regard to the Amphibia, however, there are some points which I have lately discovered that are of great importance.

As to the abortion of the upper part of the suspensorium in the Selachians, in such contrast with its *trifurcate* condition in the Urodeles, and its bifurcate condition in the Batrachia, I find myself, even in details, in the happiest conformity of views with Professor Huxley.

As to *Cestracion* (Huxley, 4, p. 42, fig. 6), I quite agree with him that the spiracular cartilage is the separate " otic process " (*ot.p*); and it is worthy of notice that whilst the spiracular cartilages of the Sharks are mere rays, yet they are chondrified detachments of the thin edge of the tissue that fills the primary fold in front of the first cleft.

In the Batrachia the *annulus tympanicus* is a cartilage; and at first, in the Tadpole, it is a process from the angle of the suspensorium; it becomes then a free ray, and then curves to form the tympanic ring—the *analogue* but not the homologue of the "annulus" of Man and the other Mammalia.

In some Urodeles this cartilage reappears, and in them forms an attachment to the stapes *above* the seventh nerve, or portio dura; this is seen in *Menopoma*, *Spelerpes*, *Desmognathus*. It imitates the "columella," but is not that organ, only a curiously specialized homologue of the spiracular cartilage of the Shark and the annulus of the Frog.

As to the rudiments of the pedicle and otic process seen in some Selachians, I quite agree with Professor Huxley, who shows both in an embryo of *Notidamus cinereus* (4, p. 44, fig. 9, *p.st.p*).

Gegenbaur (*op. cit.*), in his exquisite figures, shows these processes, notably in *Hexanchus* and *Heptanchus* (pl. 10. figs. 1, 2, 2′, *p*); but they are very evident in *Scymnus* and *Squatina* (pl. 11. figs. 1, 2), and are still more clear in *Centrophorus* (pl. 12, fig. 1).

I am also quite satisfied, from the study of a large number of Amphibian skulls (larval and adult), that the " pedicle " is the true primary head or apex of the suspensorium.

There are some curious points in the structure of the palatal bars worthy of note.

Gegenbaur (*op. cit.* pl. 11. fig. 1, *p*) figures in *Scymnus* a keystone piece to the pterygo-quadrate bars in front. In certain birds, especially the Picidæ, the two palatine bones are united by a tract of thin cartilage, which ossifies as a medio-palatine bone (Trans. Linn. Soc. ser. 2, vol. i. pl. 3, *m.pa*).

I spoke of the absence of a "pharyngo-pleural" element in the upper mandibular segment of the Selachians; I have described such a cartilage attached to the fore end of the pterygo-quadrate in a young specimen of the Aoxolotl (*Siredon*). A similar cartilage is very constant in the palate of Passerine birds ("Ægithognathæ," part i. pl. 55. figs. 1, 13, *t.pa*); but this, in both cases, may belong to the "antorbital."

In Birds an "os uncinatum" also often occurs, which is evidently the true homologue of the antorbital or ethmo-palatine of the Skate and of the Amphibians. Birds also possess "labials."

But, to return to the Ichthyopsida, I may mention that the Batrachia, which, like the Selachians, appeared most evidently to show that there was no proper distinct palatine arch, can now be cited as yielding what appear to me to be convincing proofs of the existence of such an arch, whose suspensorial point is the ethmoidal projection of the trabecula.

At first the suspensorium of a Batrachian is quite distinct from the trabecular bar; but soon after hatching it becomes attached both before and behind—before to the trabecular elbow, and behind to the ethmoidal region of the bar (see "Frog's Skull," pl. 5. figs. 1–4, *pg*).

If, in this condition, segmentation had taken place across this short conjugational bar, the upper half would have belonged to the trabecula, and the lower half to the suspensorium.

Instead of this, in the Frog, it grows into a long arch, which projects forward beyond its ethmoidal part, and is continuous with the suspensorium behind.

In the Toad, however, (see "Batrachian Skull," part 2, pl. 54. figs. 3, 4), it is segmented off, not only from its ethmo-trabecular attachment, but also from the pterygoid *process* of the suspensorium, and *becomes* what its counterpart is at first in the Urodeles and Skates, namely a distinct ethmo-palatine visceral piece.

C. *Comparison of the Selachian Skull with that of Ganoids and Teleosteans.*

In the lower kind of Ganoids, such as the Sturgeon (see Month. Micro. Journ., June 1, 1873, pl. 20, pp. 254–257), the skull becomes *hyostylic* in the highest degree, and the hyomandibular has its lower third segmented off, and separately ossified as a large symplectic segment.

The pterygo-quadrate cartilages are not unlike those of the Skate, but more arched, ultimately having *three* bony tracts in them, namely the pterygoid, palatine, and mesopterygoid.

But there is only a single counterpart of the two spiracular cartilages. It is an arched or convexo-concave plate, lying over the supero-posterior part of the tubular mouth; it is rounded and thick behind, and thin and angular in front, where it fits in beween the right and left pterygo-quadrate bars; it is a double "pedicle."

In *Polypterus* (Traquair, Journ. of Anat. and Phys. vol. v. plate 6), the pterygo-quadrate is a large bar of cartilage more or less ossified by a metapterygoid, quadrate, pterygoid, and mesopterygoid centre. But the top of the metapterygoid is very low down; and the hyomandibular has a small postero-superior osseous centre, and a large bony tract which takes in all the rest of the bar, without an inferior "symplectic" bony centre.

The palatine is a small ossicle, placed unconformably to the rest of the bar, at its *extreme* fore end, and in its *transverse* position answers to the ethmo-palatine bone of *Amblystoma* and the Batrachia.

In the Salmon there is much that is in conformity with what is found in the Rays, but greatly modified. The palato-quadrate arcade ("Salmon's Skull," plate 6. fig 2) is let down, so that the top, or otic process, is halfway down the hyomandibular bone; and this process is occupied by a square ossification, the metapterygoid, between which and the base of the inverted triangle of bone below (the quadrate) there is a wide tract of cartilage. This tract mounts up in front, and passes into a rounded boss, the arrested pedicle. Then, further forwards, the cartilage is reduced to a very narrow tract; and this wedge of cartilage, between the mesopterygoid above and the pterygoid below, shows how far the *pterygoid cartilaginous process* grew from the front of the quadrate region of the suspensorium. That tract answers to the fore part of the upper jaw of a Selachian.

But the rest of the bar, where the cartilage breaks away from between the two plates of bone (*pg*, *m.pg*), is attached by a short pedicle to the ethmoid, and then grows forwards as a massive præpalatine rod, with a swollen boss for the head of the maxillary. All this part is formed out of the originally distinct ethmo-palatine rod (ibid. pl. 2. figs. 6, 7, *pp.g*).

Curious and instructive it is to find that at first, as in the Skate and Urodele, this distinct præoral pleural arch is thick above and grows backwards to a point.

By the middle of the second week after hatching, the fry of the Salmon shows a præpalatine spur, which becomes so large in the adult, and which is so well seen in the separated ethmo-palatine of *Bufo vulgaris*.

The hyostylic skull of the Salmon is easily seen to be a further specialization of what is so remarkable in the skull of the Skate—although in the details of the segmentation of the top of the hyoid arch there is some difference, the hyomandibular being an independent nucleus in the Skate, and arising in the Salmon by longitudinal splitting of the primary bar ("Salmon's Skull," plate 2. fig. 3, *h.m*, *ch*).

In the Skate (Pl. XLI. fig. 4, *i.h.l*) the posterior division of the hyoid is attached *above* to the postero-superior angle of the hyomandibular by an interhyal ligament.

This state of things is seen in Salmon embryos just before hatching (ibid. pl. 2. figs. 6, 7, *h.m*, *ch*, *third stage*); but in the adult (ibid. pl. 6. fig. 2) the hinder moiety (*ep.h*, *c.h*) is suspended from the synchondrosis between the long hyomandibular and the short symplectic, exactly opposite the quadrato-metapterygoid synchondrosis.

There this kind of specialization, the *hyostylic*, is carried to its uttermost degree, and the articulation of the two main hyoidean moieties is but little above that of the mandible and its pier; yet the whole is but an exaggeration of what is seen in the Skate.

The structure just described may be found in by far the greater number of Tele-

ostean fishes; but in the Eel (*Anguilla acutirostris*) and its congeners there is a less degree of specialization of the Raiine type of face.

In small, *white* young of that species, $2\frac{2}{3}$ inches in length (the gift of Mr. F. Buckland; see 'Nature,' June 22, 1871, pp. 146–148), I find the following modifications of the Teleostean face.

The hyomandibular has a most extensive *otic* region, the front and hinder head being far apart, and under the latter the opercular knob. This *transverse* top grows downwards, as an arcuate rod, with its convexity behind.

It is ossified by the hyomandibular centre down to the bent part; then there is a large tract of cartilage, which has its pointed forward end capped by a symplectic bony sheath, which passes inside the quadrate in front of it.

On the back of the middle of the synchondrosial tract there is an interhyal nucleus of cartilage, from which a ligament grows; and to this ligament the hyoid cornu is suspended. This cornu does not separate off into a hypohyal below; and the epi- and ceratohyals completely ossify the rod, largely overlapping each other.

Below its front condyle the hyomandibular sends forwards and downwards two strong sharp spines of *periosteal* bone; and these embrace the ascending but lowered head of of the mandibular suspensorium, which is a shortish straight rod, unossified above and below.

Its ossification is a cylindrical, ectosteal quadrate; and the apex receives no metapterygoid bony centre.

As in the Urodeles, there are a bony and a cartilaginous pterygoid; the former is a delicate f-shaped style, pedate behind, to run up the front face of the suspensorium.

The *cartilaginous* pterygoid (*r. pg*, rudiment of pterygoid) is a triangular process, growing from the front of the quadrate bar below, exactly as in the larva of every known kind of Caducibranchiate Urodele, as well as in certain Perennibranchiates; it is also the arrested homologue of the part which, in the Salmon, coalesces with the ethmopalatine, and also of the extended limb of the "upper jaw" of the Selachian.

The ethmopalatine is suppressed in the Eel, and its skull is as simple as that of a Snake or of the *Proteus*.

But a skull whose structure has long puzzled me, namely that of the Siluroid *Clarias capensis*, comes in as the most demonstrative proof of the existence of a præoral postnasal visceral arch.

As in the Eel and its congeners, the hyomandibular of *Clarias* has an extensive *otic* region; and, as in the Eel, the fore part of that bone develops an extraordinary amount of periosteal bone in front, which aborts, or coalesces with the metapterygoid.

The whole pterygo-quadrate arcade is a broad, flat, almost transverse plate, not ascending behind into an otic process, but being angular behind and above the quadrate condyle, and strongly wedged in between the foregrowths of the hyomandibular and the separate symplectic bone.

This obliquely placed plate runs almost directly forwards, and articulates by its antero-superior bony centre to the outer angle of the crescentic dentary fore edge of the vomer—a constant relation of these bones in Carinate Birds; it is seen also in *Anguis* and *Hatteria*.

But the thin lamina of cartilage that formed the "model" for these three bones—the quadrate (its front part), the pterygoid—and the mesopterygoid, is totally independent of the palatine bone; and the whole arcade is very loosely connected by ligament to that bone.

The palatine (or rather "ethmo-palatine") is a thick rod of ossified cartilage, lying above the pterygo-quadrate plate, and reaching far in front of it. Behind, it ends above the fore margin of the quadrate ossification, and in front reaches nearly to the angle of the præmaxillary.

In front it carries the arrested maxillary—the filament-bearer—which is wedged between it and the præmaxillary; whilst the foremost of the two præorbital ossicles, that which becomes the "septomaxillary" of the *air-breathers*, rides upon its fore end and also upon the fore end of the little maxillary.

The most projecting part of the massive lateral ethmoid is a little in front of the middle of this ethmo-palatine bar; but the ethmo-palatine *process* is represented by ligament, and the bone is everywhere loosely attached to the surrounding bones.

Everywhere, above the Skate and its congeners, the exoskeletal bone that is related to the "ethmo-palatine," as its proper splint, is the maxillary. This may be equally well seen in Teleostean Fishes, Urodeles, Anura, and Carinate Birds.

In bringing out this ethmo-palatine element of the face into bold relief, I have done no violence to Nature, but only to my own confused and confusing prejudices.

No "labial" element or "extravisceral" cartilage has ever been allowed to come into my way in considering the true endoskeletal elements. I have used no cutting and contriving in trying to arrange morphological segments; the parts are allowed to tell their own story; and listening to catch from them the least hint of their real meaning (I hold my opinions almost loosely even), I am ready to cease from the folly of my own wisdom at any moment, and adopt the truth, whenever and wherever I can unearth it[1].

DESCRIPTION OF THE PLATES.

PLATE XXXIV.

Fig. 1. *First stage.* Side view of an embryo of Dog-fish (*Scyllium canicula*), 8 lines long, seen as a transparency, × 16 diam.

[1] Whilst correcting the present paper (August 25th, 1877) I find in the Tadpole of *Rana clamata* four small *internal* branchial arches; its pouched arches are "extrabranchials," and answer to the branchial "basket" of the Lamprey.

Fig. 2. Another embryo, 11 lines long, seen as an opaque object, × 14 diam.
Fig. 3. The same, seen from below, × 14 diam.
Fig. 4. The same, seen from above, × 14 diam.
Fig. 5. The same, in longitudinal section, × 14 diam.
Fig. 6. Part of fig. 1, × 24 diam.

PLATE XXXV.

Fig. 1. *First stage.* Side view of *Pristiurus* embryo, $\frac{2}{3}$ of an inch long, × 20 diam.
Fig. 2. The same, from below, × 20 diam.
Fig. 3. Dissection, from above, of the same embryo, × 20 diam.
Fig. 4. Dissection, from above, of a larger embryo ($\frac{3}{4}$ of an inch long), × 20 diam.
Fig. 5. Dissection, from above, of an embryo of *Scyllium canicula* (13 lines long), × 20 diam.
Fig. 6. *Second stage.* Dissection, from above, of a larger embryo of *Scyllium canicula* $1\frac{1}{3}$ inch long, × 14 diam.
Fig. 7. The same, dissected from below, × 14 diam.
Fig. 8. Part of fig. 6, × 30 diam.

PLATE XXXVI.

Fig. 1. *Second stage.* Side view of head of *Scyllium canicula*, partly dissected, from an embryo, 1 inch 2 lines long, × 12 diam.
Fig. 2. Vertical section of a somewhat larger embryo, × 14 diam.
Fig. 3. *Third stage.* Chondrocranium of a two-thirds-ripe embryo of the same fish, 1 inch 8 lines long, seen from above, × 10 diam.
Fig. 4. The same object, seen from below, × 10 diam.
Fig. 5. The cranium without the facial arches; side view, × 10 diam.
Fig. 6. Section of head of the same, × 14 diam.

PLATE XXXVII.

Fig. 1. *Third stage*, continued. Skull of the same, seen from below, × 10 diam.
Fig. 2. *Fourth stage.* Adult *Dog-fish*, upper view of the skull, × $1\frac{1}{2}$ diam.
Fig. 3. The same, with facial arches removed, under view, × $1\frac{1}{2}$ diam.
Fig. 4. Section of head of the same, × $1\frac{1}{2}$ diam.
Fig. 5. Part of same object, × $5\frac{1}{2}$ diam.

PLATE XXXVIII.

Fig. 1. Skull of adult Dog-fish, seen from below, × $1\frac{1}{2}$ diam.
Fig. 2. Side view of same, × $1\frac{1}{2}$ diam.
Fig. 3. End view of same, × $1\frac{1}{2}$ diam.
Fig. 4. Vertieal section of cranium, × $1\frac{1}{2}$ diam.

PLATE XXXIX.

Fig. 1. Skate. *First stage.* Side view of embryo of *Raia maculata*, 1 inch 4 lines long, 7 weeks old, from the deposit of the egg-pouch, × 14 diam.

Fig. 2. Same object, with facial arches shown, × 14 diam.

Fig. 3. Part of same, × 20 diam.

Fig. 4. Under view of same embryo, × 14 diam.

Fig. 5. Upper view of same, × 14 diam.

Fig. 6. Part of fig. 5, Plate XXXV., *Scyllium*, × 40 diam.

PLATE XL.

Fig. 1. *Second stage.* Under view of fore part of an embryo of *Raia maculata*, 3 months from deposit of egg-pouch, × $3\frac{1}{2}$ diam.

Fig. 2. Upper view of same, × $3\frac{1}{2}$ diam.

Fig. 3. Side view of same, × 7 diam.

Fig. 4. Skull of same, seen from above, × 5 diam.

Fig. 5. Same object, seen from below, × 5 diam.

Fig. 6. Cranium of same, from below, × 5 diam.

Fig. 7. Part of fig. 3, Plate XXXV. × 40 diam.

PLATE XLI.

Fig. 1. *Third stage.* Section of cranium of *Raia clavata* (nearly ripe embryo), × 7 diam.

Fig. 2. Transverse section of same through nasal sacs, × 14 diam.

Fig. 3. *Fourth stage.* Skull of adult *Raia clavata*, from above, × $1\frac{1}{2}$ diam.

Fig. 4. The same, side view, × $1\frac{1}{2}$ diam.

Fig. 5. Hyoid arch, with "branchial rays" of same, inner view, × $1\frac{1}{2}$ diam.

PLATE XLII.

Fig. 1. *Third stage*, continued. Section through antorbital region of ripe embryo of *Raia clavata*, × 14 diam.

Fig. 2. A similar section of same, through the eyes, × 14 diam.

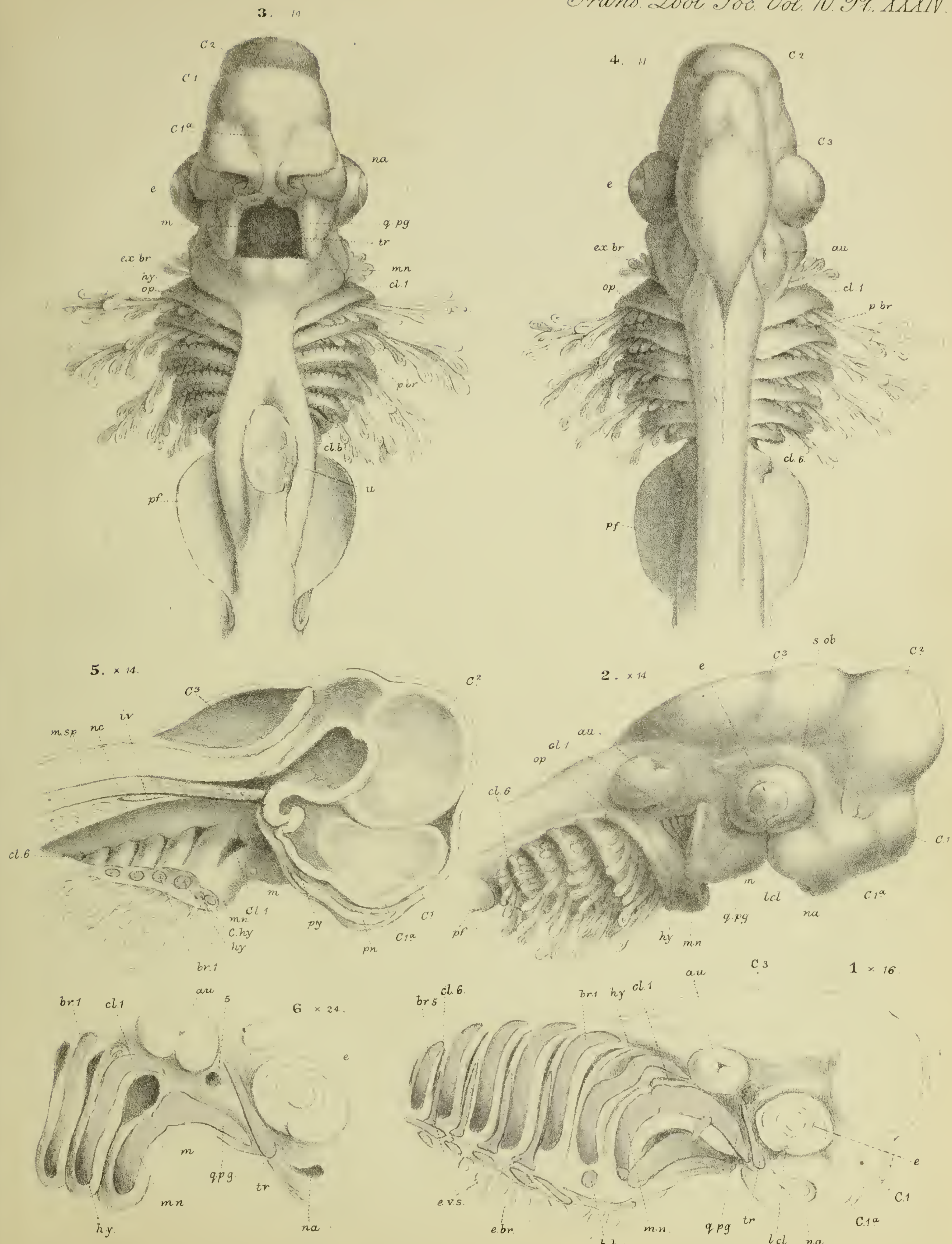
Fig. 3. Another section through auditory sacs, × 14 diam.

Fig. 4. *Fourth stage* continued. Under view of skull of adult *Raia clavata*, × $1\frac{1}{2}$ diam.

Fig. 5. Transverse section of skull of Dog-fish, 3rd stage, through the eyeballs, × 14 diam.

Fig. 6. Another section, rather oblique, in postorbital region, × 14 diam.

Fig. 7. A third section, through the auditory capsule, × 14 diam.



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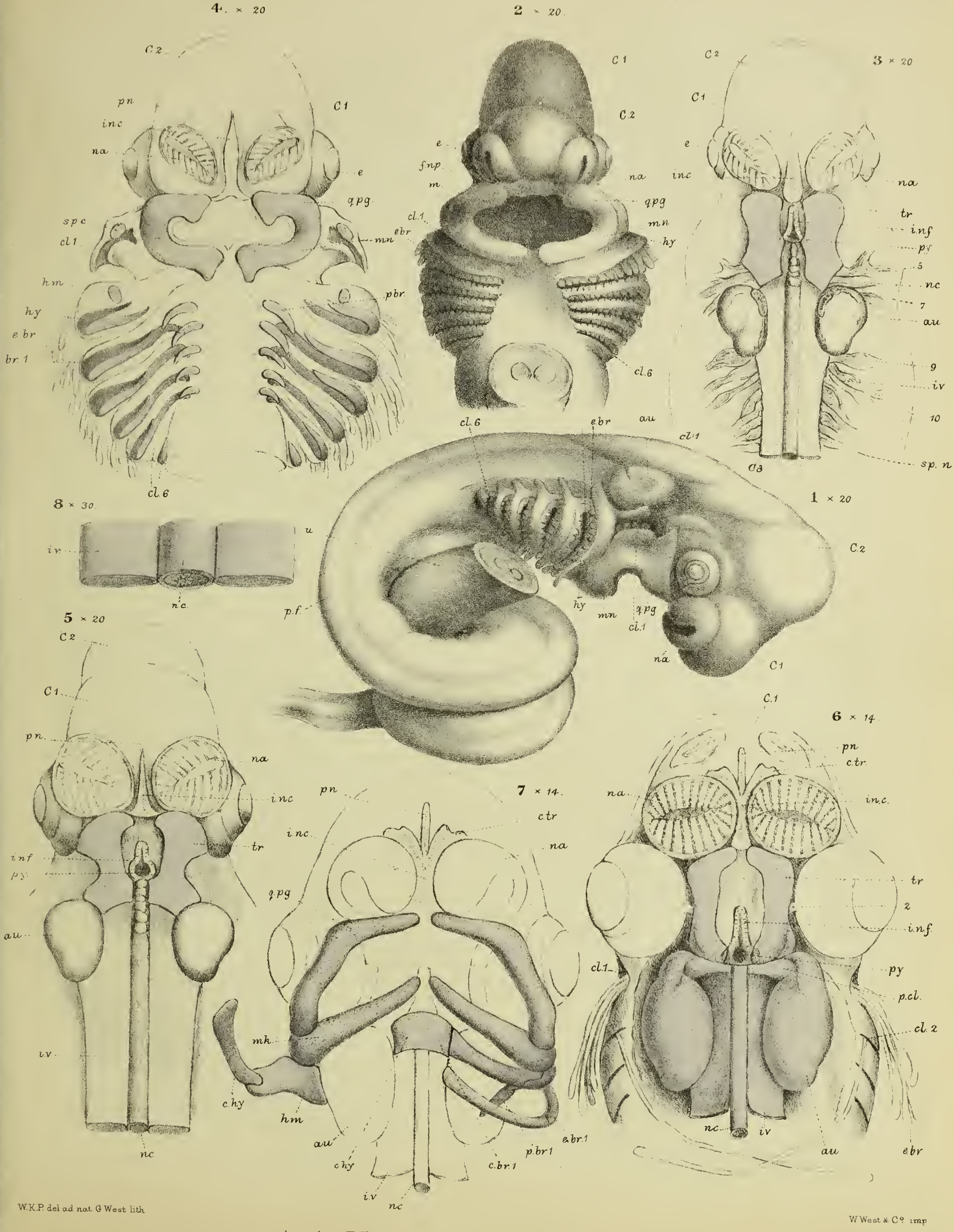

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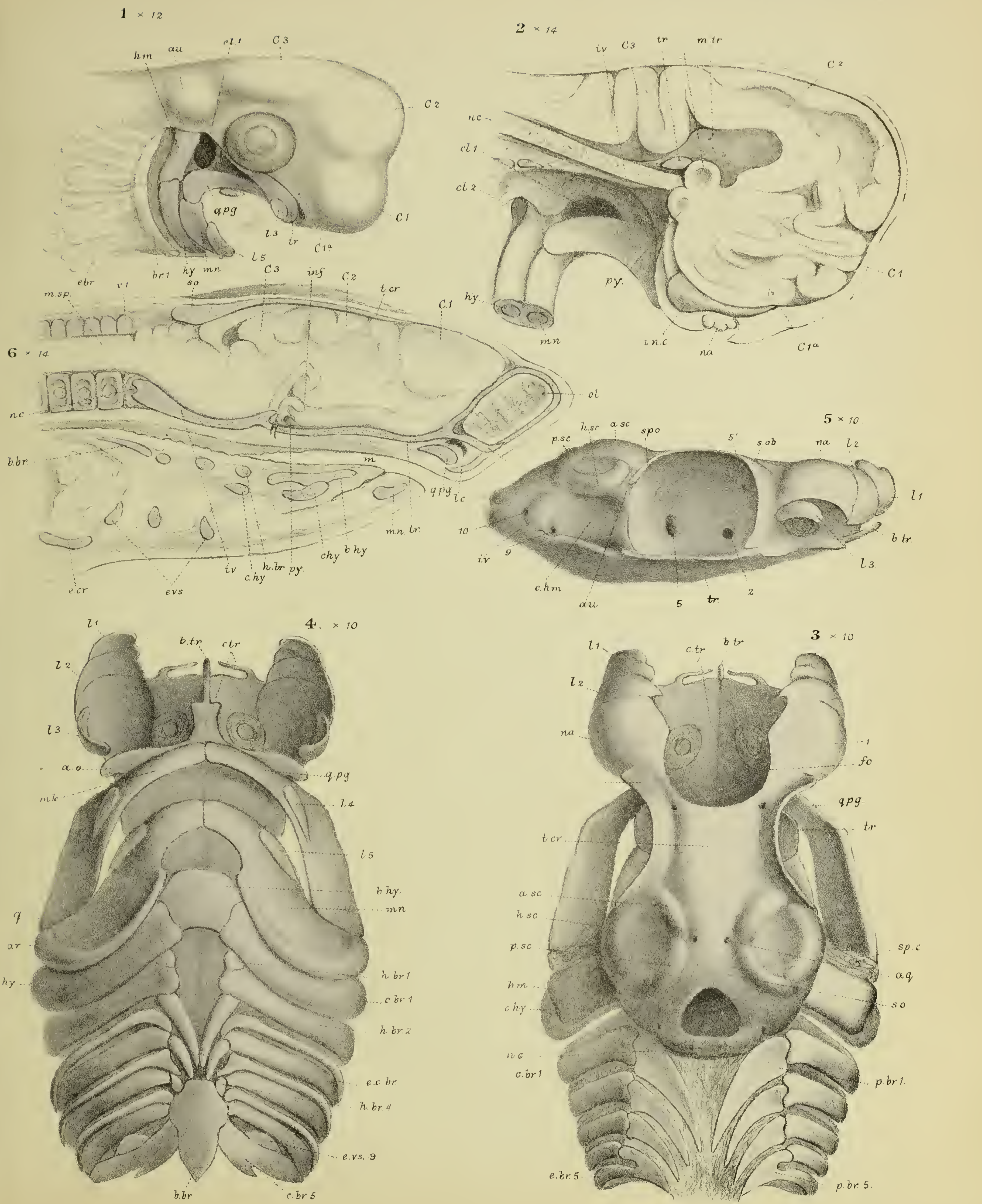

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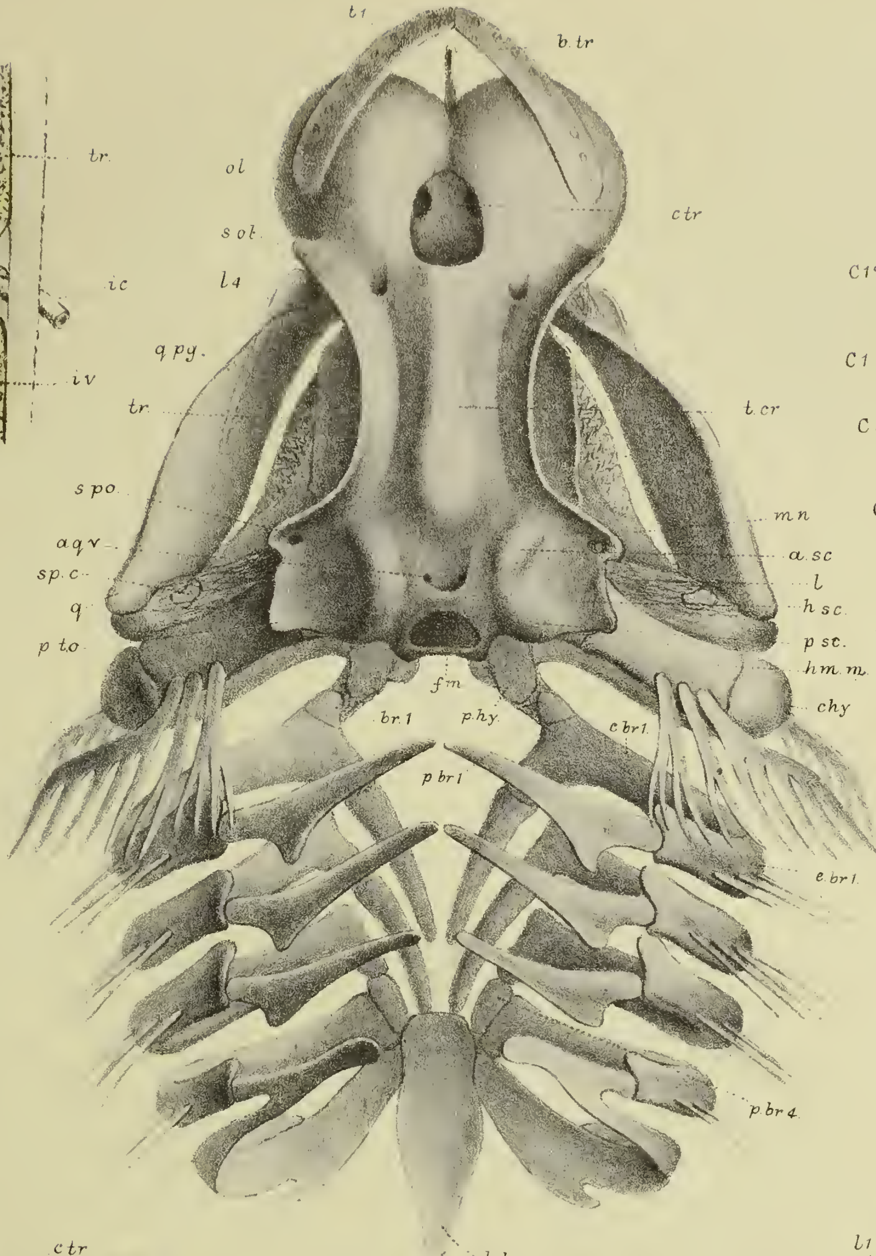

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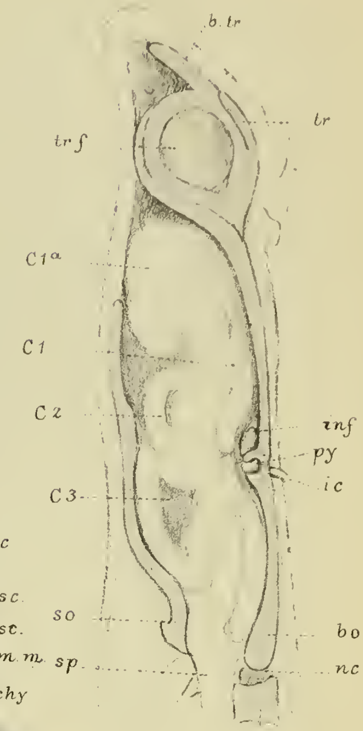

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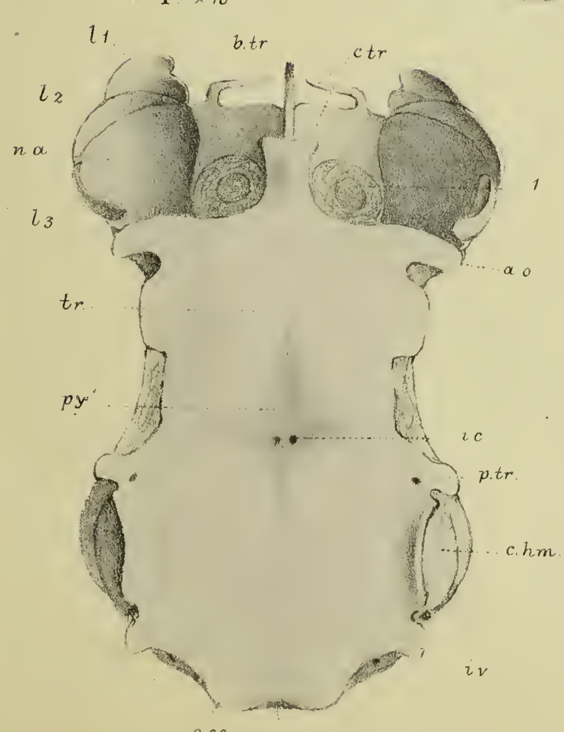

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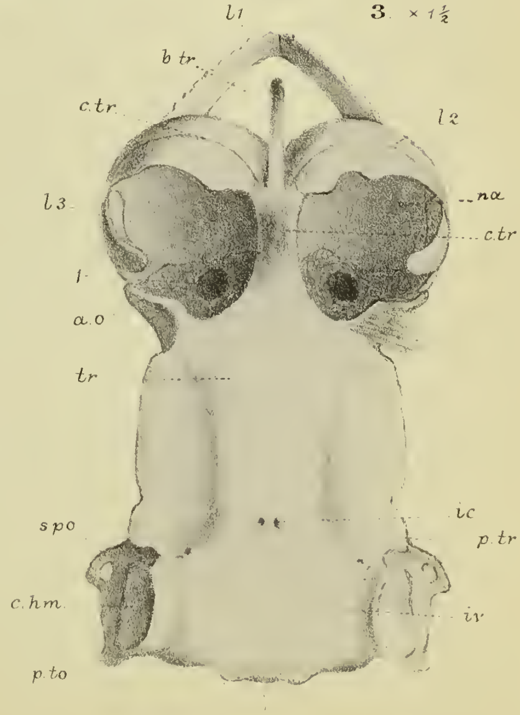

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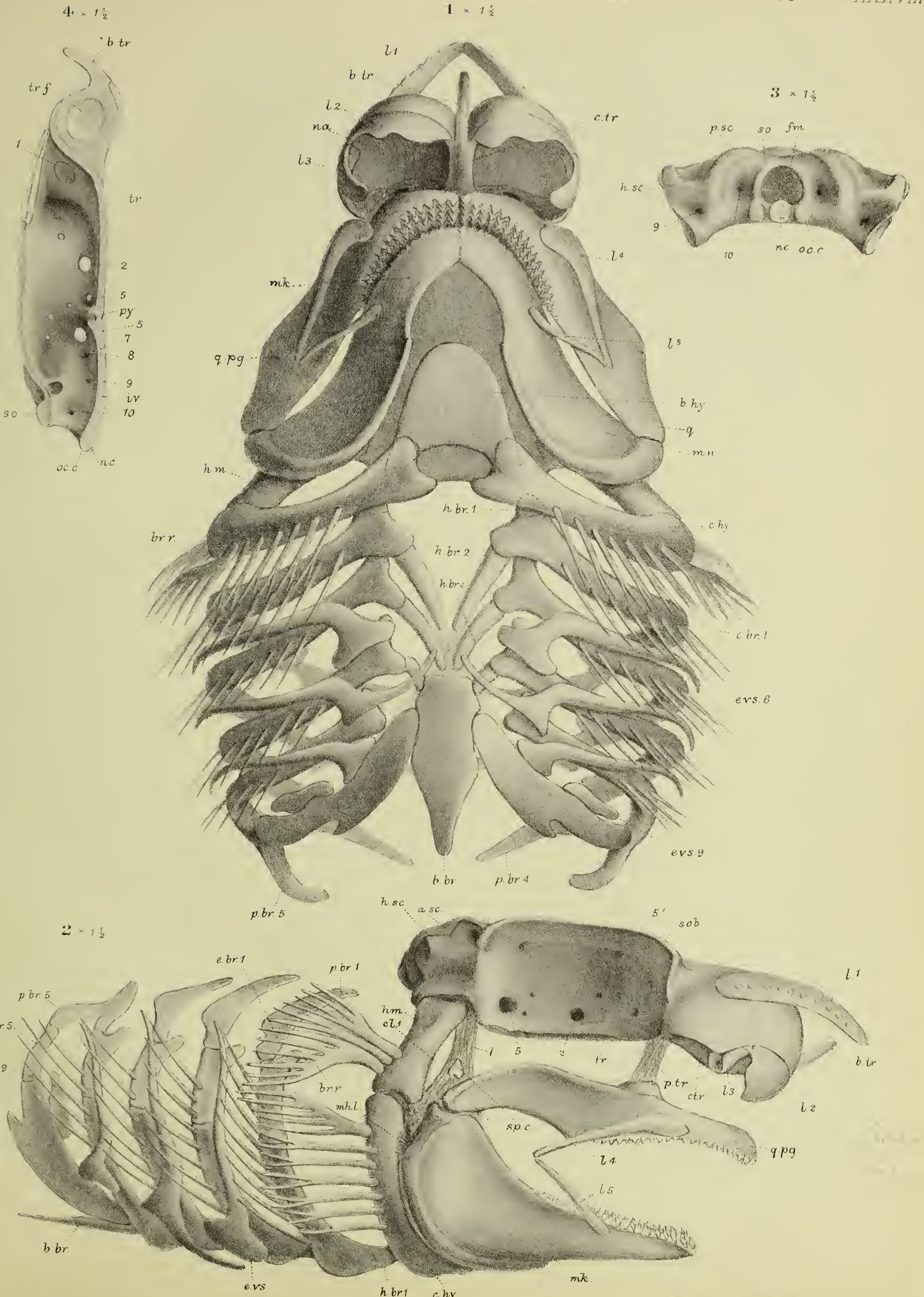

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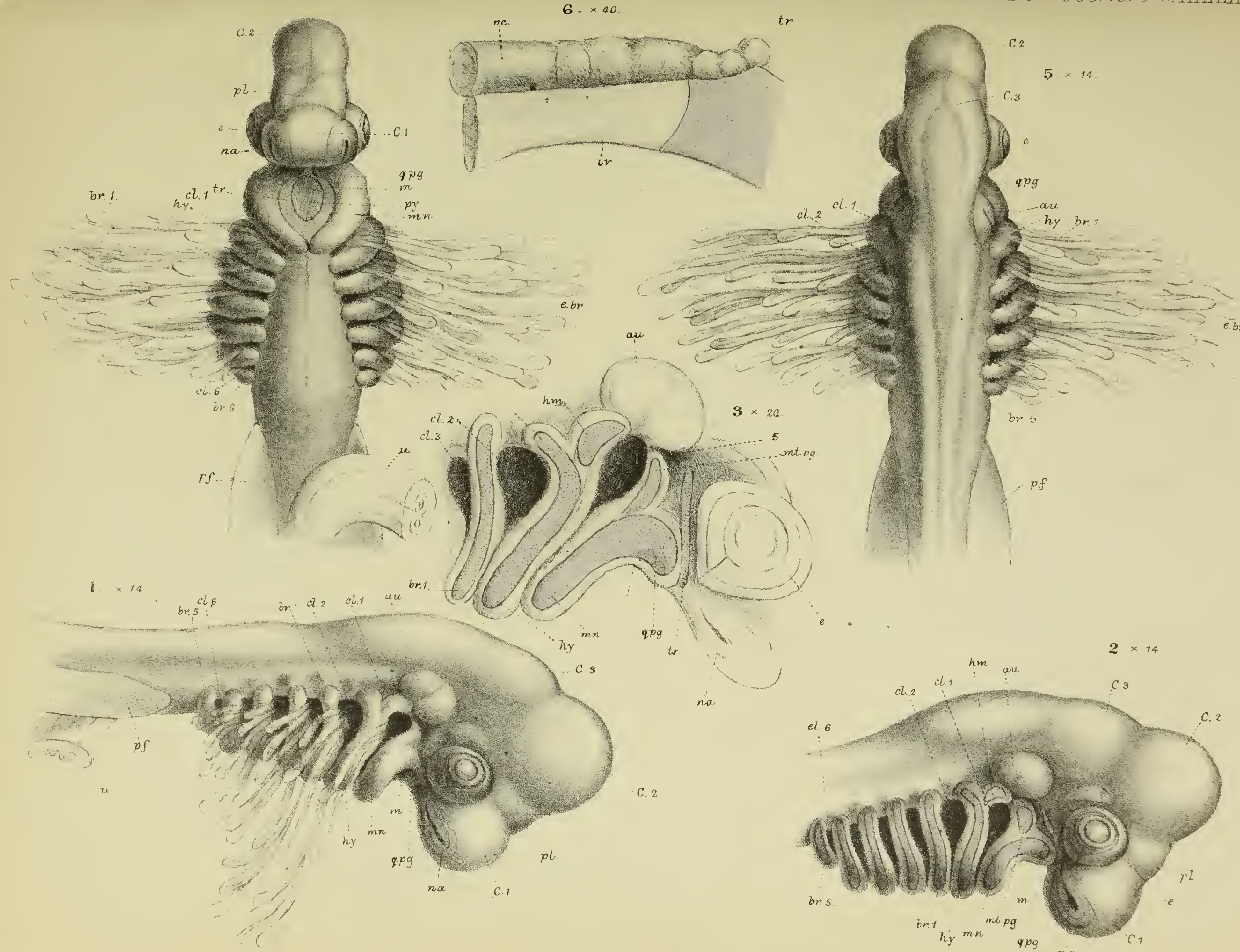

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1—5. RAIA MACULATA 6. SCYLLIUM CANICULA

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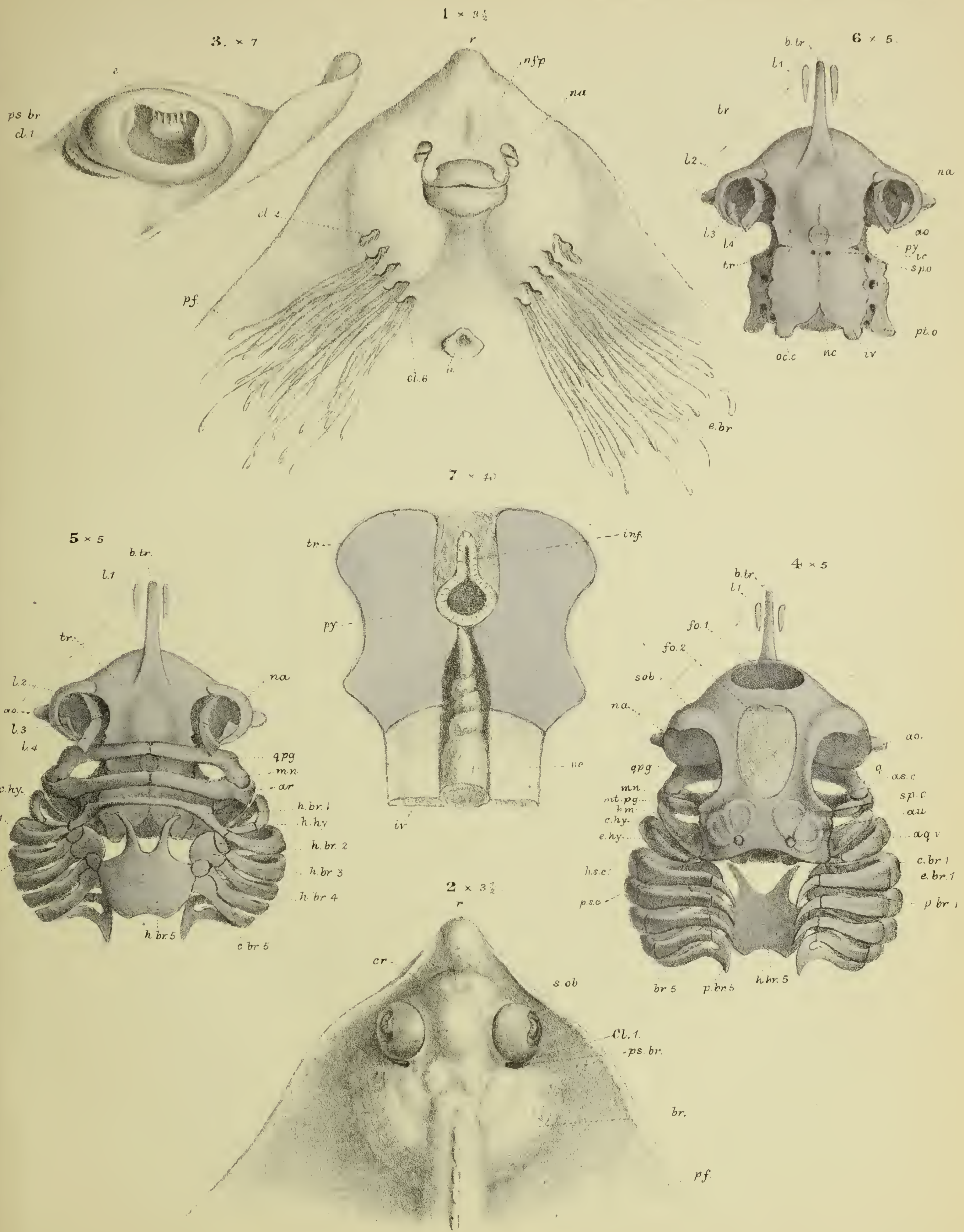

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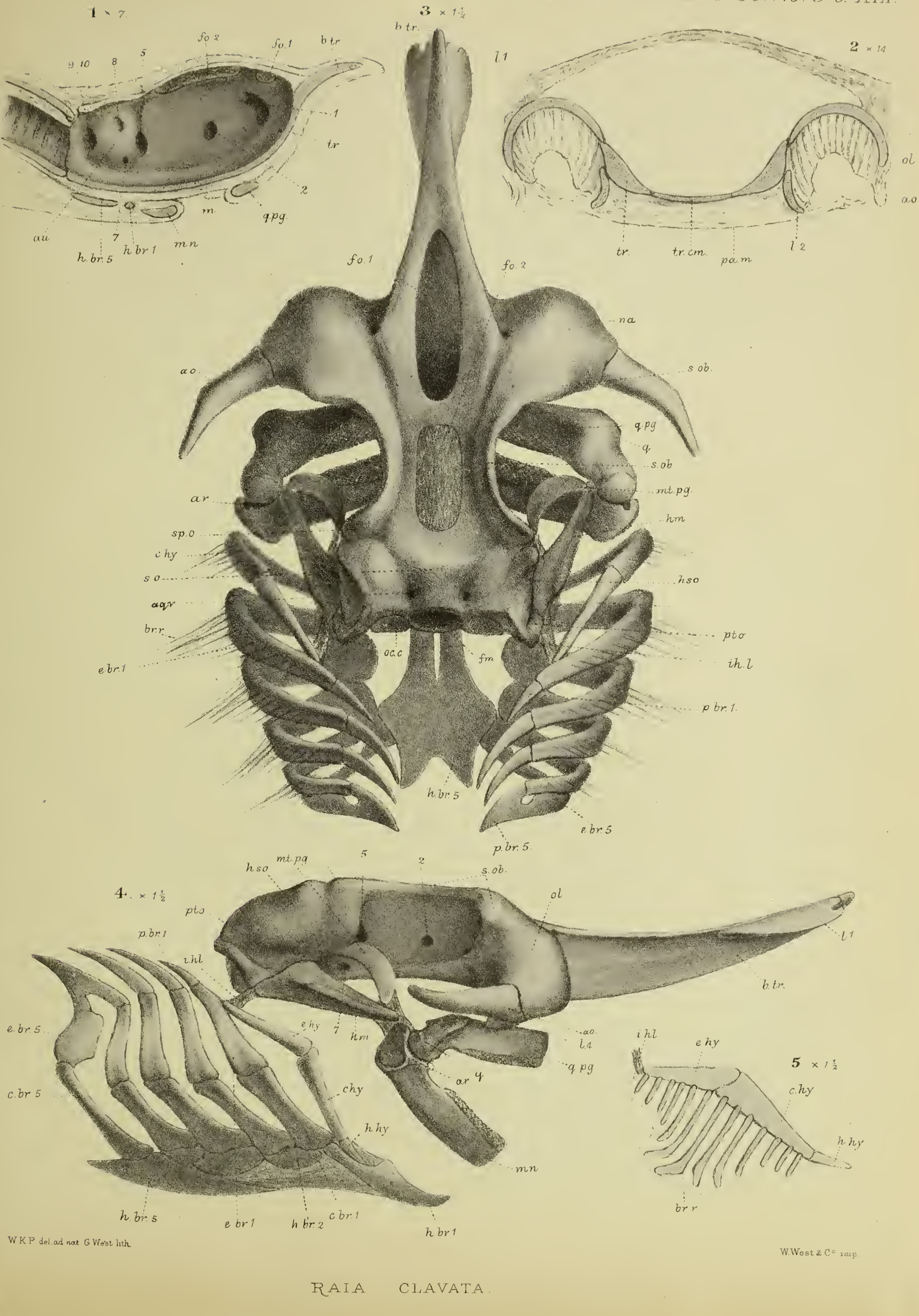

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RAIA CLAVATA.

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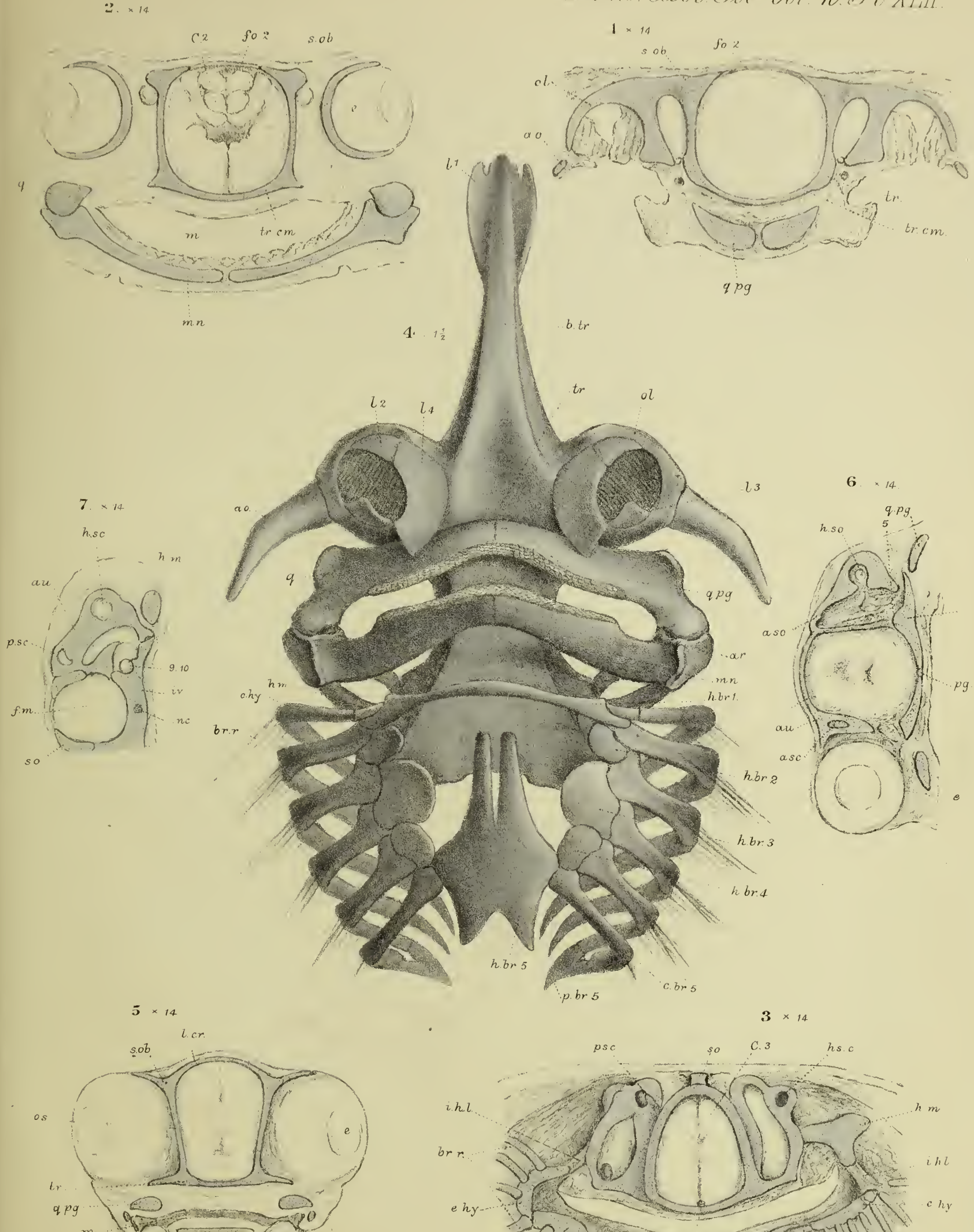

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ON

THE STRUCTURE AND DEVELOPMENT

OF THE

SKULL IN STURGEONS

(ACIPENSER RUTHENUS AND A. STURIO).

BY

WILLIAM KITCHEN PARKER, F.R.S.

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III. *On the Structure and Development of the Skull in Sturgeons* (Acipenser ruthenus *and* A. sturio).*

By William Kitchen Parker, *F.R.S.*

Received April 14,—Read May 5, 1881.

[Plates 12–18.]

INTRODUCTION.

Several years ago the late Mr. William Lloyd procured for me from Hamburgh seventeen young Sturgeons (*Acipenser sturio*); these were from 7 to 8 inches in length. Valuable as these specimens were, they were far too much developed for embryological purposes; and no pains were spared by me to obtain, if possible, newly-hatched embryos and small "fry" of this type.

More lately it was suggested to me by Mr. Balfour that I should write to Professor W. Salensky, of Kasan, who had been working at the development from the egg of *Acipenser ruthenus*, the small Sturgeon or "Sterlet."† My application to him was promptly and most kindly responded to, and in a short time I received a considerable number of newly-hatched and very small young of that species, ranging from 5½ to 14½ millims. in length. Half these were for Mr. Balfour, and the rest for me. His researches are embodied in that inestimable work, the second volume of his 'Comparative Embryology;' mine are here offered to the Society in the accustomed form.

I purposely refrain at present from working out the structure and development of the trunk and limbs (I have laboured at these regions, and shall be ready to resume that part of my work when this is done); but other workers are from time to time taking up those parts, and when once the cephalic skeleton is mastered what remains will be a comparatively easy task.

I am more anxious to be prepared for my own limited work by acquiring a thoroughly clear conception of the embryology of each type; in this my best helper is Mr. F. M. Balfour. Professor Huxley is, and always has been, my most valued critic and counsellor in all that relates to broad and philosophical views of animal life generally, and of the life of the Vertebrata in particular.

* The skull described in my last paper as that of *Discoglossus pictus* (Phil. Trans. 1881, Plate 20, figs. 7–11, p. 112) was prepared from a badly-preserved, half-grown *Rana esculenta*. I am indebted for this correction, and for a genuine *Discoglossus*, to M. Boulenger.

† This species rarely exceeds the length of 3 feet (Günther, 'Study of Fishes,' p. 361).

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First Stage.—Newly-hatched embryos of Acipenser ruthenus *from* $5\frac{1}{2}$ *millims. to* $6\frac{1}{2}$ *millims. in length.*

The specimens figured by me (Plate 12, figs. 1–3) are rather smaller than the one figured by Mr. BALFOUR ('Comp. Embryol.,' vol. ii., p. 88, fig. 53) which measured 7 millims. in total length, but his description may serve for mine, which were nearly as much developed as his slightly larger specimen.

After describing the development of the embryo, Mr. BALFOUR explains its peculiar outspread form in its unhatched condition (*op. cit.*, p. 86, fig. 52), and says:—"The further changes which take place are, in the main, similar to those in other Ichthyopsida, but in some ways the appearance of the embryo is, as may be gathered from fig. 52, rather strange. This is mainly due to the fact that the embryo does not become folded off from the yolk in the manner usual in the Vertebrates; and as could be shown in the sequel, the relation of the yolk to the embryo is unlike that in any other known Vertebrate. The appearance of the embryo is thus something like that of an ordinary embryo slit open along the ventral side and then flattened out. Organs which properly belong to the ventral side appear in the lateral parts of the dorsal surface. Owing to the great forward extension of the yolk the heart (fig. 52, B) appears to be placed directly in front of the head." Then, after describing the progress made in the development of the brain and organs of special sense, Mr. BALFOUR says:—"At the sides of the cephalic plate the visceral arches make their appearance, and in fig. 52, A and B, there are shown the mandibular (*Md.*), hyoid (*Ha.*), and first branchial (*Br.*) arches, with the hyo-mandibular (spiracle) and hyo-branchial clefts between them. They constitute peculiar concentric circles round the cephalic plate, their shape being due to the flattened form of the embryo already alluded to." And then, further on (p. 88) our author says:—"Before hatching, the embryo has to

a small extent become folded off from the yolk both anteriorly and posteriorly; and has also become to some extent vertically compressed. As a result of these changes, the general form of its body becomes much more like that of an ordinary Teleostean embryo. The general features of the larva after hatching are illustrated by figs. 53, 54, and 55. Fig. 53 represents a larva of about 7 millims., and 54 a lateral and 55 a ventral view of a larva about 11 millims.* There are only a few points which call for special attention in the general form of the body. In the youngest larva figured" [fig. 53, 7 millims. long; and see also Plate 12, figs. 1–3 of the present paper of somewhat younger larvæ] "the ventral part of the hyomandibular cleft is already closed: the dorsal part of the cleft is destined to form the spiracle (*sp.*). The arch behind is the hyoid, on its posterior border is a membranous outgrowth, which will develop into the opercular membrane. In the older larvæ a very rudimentary gill appears to be developed on the front walls of the spiracular cleft, but I have not succeeded in satisfying myself about its presence; and rows of gill papillæ have appeared on the hyoid, and the true branchial arches (figs. 54 and 55, *g*)." [The mandibular gill, about which Mr. BALFOUR speaks doubtfully, is according to my observations a thickened mass of hypoblastic cells lining the front wall of the first or "spiracular" cleft. This mass is crescentic (Plate 12, figs. 2, 4, and 7, cl^1.), and is slightly grooved along its hinder margin; on each side of this groove the low ridges are imperfectly divided into little rounded masses, which appear to me to be, evidently, the rudiments of branchial papillæ; at the lowest computation, this soft, tuberculate mass of cells is homologous with the tracts of cells which do develop into branchial papillæ in the Elasmobranchii.] "The biserially-arranged gill papillæ of the true branchial arches are of considerable length" [see Plate 12, figs. 4–9], "and are not yet covered by the operculum, but they do not form elongated thread-like external gills like those of the Elasmobranchii. The oral cavity is placed on the ventral side of the head; it has a more or less rhomboidal form. It soon however (fig. 55) becomes narrowed to a slit with projecting lips, which eventually becomes converted into the suctorial mouth of the adult. The most remarkable feature connected with the mouth is the development of provisional teeth (fig. 55) on both jaws. These teeth were first discovered by KNOCK ('Die Beschr. d. Reise z. Wolga Behufs. d. Sterlettbefructung,' Bull. Soc. Nat., Moscow, 1871). They do not appear to be calcified, and might be supposed to be of the same nature as the horny teeth of the Lamprey. They are, however, developed like the teeth, as a deposit between a papilla of subepidermic tissue and an epidermic cap. The substance of which they are formed corresponds morphologically to the enamel of ordinary teeth. As they grow they pierce the epidermis and form hollow spine-like structures with a central axis filled with subepidermic mesoblastic cells. They dis-

* These do not correspond precisely to the specimens worked out by me, and of which I also have given figures illustrating the outward form. My first Stage includes larvæ from $5\frac{1}{2}$ millims. to $6\frac{1}{2}$ millims. in total length; Stage two, $8\frac{1}{2}$ millims. to $9\frac{1}{2}$ millims.; and Stage three, $13\frac{1}{2}$ millims. to $14\frac{1}{2}$ millims. The largest larva of this species in those sent to me was $14\frac{1}{2}$ millims. ($\frac{7}{12}$ths of an inch) in total length.

appear after the third month of larval life. In front of the mouth two pairs of papillæ grow out, which appear to be of the same nature as the papillæ in the suctorial disc of Lepidosteus (figs. 54, 55, p. 89). They are very short in the embryo, represented in fig. 53. Soon, however, they grow in length (figs. 54 and 55, *st.*)" [Plate 12, figs. 4, 5, 7, 9], "and it is" [*more than*] "probable that they become the barbels, since both sets of structures occupy a precisely similar position."

"The openings of the nasal pits are at first single, but the opening of each becomes gradually divided into two by the growth of a flap on the outer side (fig. 54, *ol.*)" [Plate 12, figs. 4, 7, 9, *ol.*]. "It is probable that the two openings of each nasal sack, so established in these and in other Fishes, correspond to the external and internal nares of the higher Vertebrata. At the time of hatching there is a continuous dorso-ventral fin" [Plate 12, figs. 1, 2], "which by atrophy in some parts, and hypertrophy in other parts, gives rise to all the impaired fins of the adult, except the first dorsal and the abdominal. The caudal part of the fin is at first symmetrical, and the heterocereal tail is produced by the special growth of the ventral part of the fin combined with an atrophy of the dorsal part."*

Referring the reader to Mr. Balfour's work and to my own plates, I shall now simply describe the figures of the general form of the first stage, and then those of the second and third, in which also will be given a detailed account of their skeletal structures.

The fourth, fifth and sixth stages will be of the other species (*A. sturio*), and that in a thoroughly metamorphosed condition.

The smallest of my specimens ($5\frac{1}{2}$ millims. long, Plate 12, fig. 1) is intermediate between figs. 52 and 53 of Mr. Balfour (*op. cit.*, pp. 87, 88); the original of his fig. 52 (A and B), may be found in Professor Salensky's Russian work (plate 7, figs. 56 and 58), whilst his fig. 53 is only slightly larger than my second specimen (Plate 12, figs. 2 and 3).

In the smallest specimen, scarcely hatched at the time when it was put into the spirits, the large hind-brain (C^3.) and the lesser mid- and fore-brain (C^2., C^1.) are seen arranged in an accurate series. The auditory sac (*au.*) is below and behind the wide, front part of the hind-brain, the eye (*e.*) below and between the fore- and hind-brain, and the olfactory sac (*ol.*) on the side of and below the fore-brain, in front of the eye. The mouth (*m.*) is a considerable rhomboidal space on the ventral aspect of the head, and behind it we see three folds, two clefts, and a general hollow space behind the third fold. These folds are the rudiments of the mandible, hyoid, and first branchial (*mn.*, *hy.*, br^1.), the clefts are the hyomandibular (cl^1.) and the hyo-branchial (cl^2.), and the fossa behind leads to the tissues that are preparing to form the rest of the branchial arches with their intervening clefts. The last third of the spinal region is

* I am glad to be able to give, and the reader will not be sorry to have, an account of these early larvæ in Mr. Balfour's own words. Of course I have been over the same ground, but my work has been made much easier by my friend's kindness in sending me his proofs as soon as they were in type.

behind the anus (*an.*); it is the tail, and the intestinal opening is but a small distance behind the huge enlargement caused by the yolk-mass; that mass is three-fifths the length of the embryo. A vertical line drawn through the hind-brain and eye-ball would bisect a special enlargement in front of the yolk-mass. This enlargement, caused by the heart (*h.*), would be partly in front of that line, and looking at the embryo from the upper end of the line we should see the heart lying *in front of the head.*

The liver (*l.*) would be behind the lower end of the line, for most of the yolk-mass which is included in the rudimentary stomach lies *in front of the liver*, contrary to what takes place in the Lamprey, Frog, Elasmobranch, and the Amniota (BALFOUR, *op. cit.*, p. 90, fig. 56). According to that excellent observer "the peculiar flattening out of the embryo on the yolk is due to the mode in which the yolk becomes enveloped by the hypoblast" (p. 91).

In an embryo more developed, but slightly smaller (Plate 12, figs. 2, 3, $6\frac{1}{2}$ millims. long) than that figured by Mr. BALFOUR (his fig. 53 was 7 millims. long), the yolk-mass is only one-third the length of the embryo—in the last it was half as long—and the tail is now also about one-third the length of the whole larva. The head is now fairly free from the yolk-mass, at least as far as to the hyoid fold (*hy.*), but the heart (*h.*) is a very short distance behind the mouth (*m.*), and the end of the intestine (*an.*) is seen to be three times as far from the yolk-mass (*y.*). The tail is at present perfectly diphycercal; the notochord running along the middle of the upturned tail, and the azygous fin is equally above and below the axis.

The mouth (fig. 3, *m.*) is a crescentic slit, with a small anterior bay in the middle of its anterior convex margin, and with a definite labial rim. In front of the oral opening and under the fore-brain (C^1.), behind a transverse ridge that passes from side to side parallel with the mouth, there are two pairs of pupiform enlargements with their narrow ends behind, and those of each pair approximated; these are the rudiments of the barbels (*bb.*). There are four visceral folds with their clefts, the two anterior larger folds being the mandibular and the hyoid; from the latter a free edge is growing, the opercular fold (*op.*); between the two bars the first (or hyomandibular) cleft (cl^1.) is closed ventrally, already, its permanent uppermost part will be the spiracle. The convex front lip of that limited cleft is thickening inside, and tends to produce a mandibular gill. The nasal sac (*ol.*) is still a shallow pouch with a thickened rim, the outer coats of the eye (*e.*) are closing over the lens, and the auditory sac (*au.*) is a smallish oval mass showing no evident involution.

In this larger embryo the basis-cranii and visceral arches are still composed of "embryonic cartilage;" these skeletal structures can be better studied in somewhat more advanced larvæ.

Second Stage.—Larva of Acipenser ruthenus, *from* $8\frac{1}{2}$ *to* $9\frac{1}{2}$ *millims. in length.*

The larvæ at this stage have a very *Selachian* appearance (Plate 12, figs. 4–8); altogether they have made a very great advance in development since the last stage: I shall describe first the external form, then a dissection of the visceral arches, and after that a series of transverse sections.

The azygous fins are beginning to be subdivided (fig. 7); now, the axis (notochord) turns downwards behind, but the tail is still diphycercal; it has become almost as long as the trunk, measuring from the anal aperture (*an.*), so that the post-anal region is very much longer, relatively, than in the last stage (fig. 2). The azygous fin is more definite along the trunk, almost reaching as a crest to the head, and the pectoral fins (*p.f.*) that then were at most mere thickenings of the tissue, are now well-developed, free, auriform paddles.

The yolk-mass (*st.*) makes only half the bulging it did: it is now quite portable; the intestine (*in.*, *an.*) is now seen as a definite ventral cavity behind the stomach and yolk, and is nearly as long as the wide part in front.

The heart (figs. 5 and 7, *h.*) is now fairly behind the operculum (*op.*), but is still seen from the outside as a double swelling.

The mesocephalic flexure is less, and the various parts of the brain (C^1., C^2., C^3.) are very visible through the diaphanous membrano-cranium.* So also the auditory organs show clearly through the skin, and the common tube of the anterior and posterior canals (*au.*, *p.s.c.*), and the single lesser tube forming the horizontal canal (*h.s.c.*), are very apparent without dissection.

The eye-ball (*e.*) is rapidly finishing and its socket is being formed, and there is a distinct suborbital ledge. The olfactory sac (*ol.*) is lateral and close to the eye, it has acquired a very definite superficial membranous capsule; this is sending downwards a triangular flap which tends to subdivide the opening.

The "barbels" (*bb.*) are now well formed, and look in the larger specimens of this stage like formidable *tusks*; they arise from a recess in front of the upper lip, which has over it a fold of the fore face, and in front of it, below the fore brain (Plate 12, fig. 5), there is between the olfactory sacs (*ol.*) a very remarkable concavity; it is nearly circular, is as large as one of the olfactory sacs, is almost as deep, and has in front of it a crescentic fold, and on each side a lateral lip-like margin. Its somewhat produced hind margin lies between the two inner barbels, and its lateral walls run up to those barbels. In the lesser larvæ of this stage (figs. 4, 5, *m.*) the mouth is still somewhat rhomboidal, but in the larger (fig. 7) its edges come very near together. The lips are now thick and large, the front is emarginate, the hind lip has an apiculate lobe, at the mid-line, looking forward; each is armed with the small, clear, pointed teeth (*t.*).

* Through want of proper food these larvæ soon began to starve. Moreover, the spirit in which they were preserved contracted their tissues; the figures *purposely* show this contracted appearance.

There are, now, seven cartilaginous arches on each side, the two first are large, the rest smaller; they are all out of sight, more or less, the operculum hiding the two first, and the gills those behind; the clefts also are largely hidden from view by these structures.

In the smaller specimens at this stage (fig. 4) the form of the two first arches can be seen through the skin, the pterygo-quadrate bar running within the upper lip, MECKEL'S cartilage within the lower jaw, and the hyoid arch (*hy.*) inside the fore part of the opercular fold (*op.*). The opercular fold of the mandible is very limited on account of the closing in of the ventral part of the first cleft (*cl*¹.), but its serial homology with the large next fold (*op.*) is manifest. Inside it is thickened by a mass of cells from the first hypoblastic pouch, and this mass, somewhat obscurely, shows on its surface two rows of short mammillate projections—arrested gill papillæ.

But the next fold, with its lining, is greatly developed (Plate 12, figs. 4–7, *op.*), and its inner face is covered with rather long papillæ, like those which grow freely from the proper branchial arches (*br.*). Membranous, at present, this free fold of the hyoid arch is destined to contain three ganoid scutes, the upper of which (the opercular) will be one of the largest of the huge plates developed in this fish.

The rich growth of simple longish papillæ on the other arches hides them from view; these gills, however, are much shorter than those seen in the large embryos of Selachians.

When the skin and the gills are removed from the side of the head in one of the larger larvæ at this stage—9½ millims. in length—then the form of the newly chondrified bars is seen (Plate 13, fig. 6).

I have already remarked upon the *Selachian* appearance of the larvæ at this stage (Plate 12, fig. 7); a dissection, like the one under notice, displays much more than superficial Selachian characters. Even in the adult the Sturgeon has not made much advance towards the Teleostean culmination of the fish-type, but the dermal scutes have been largely dominated, in the head, by the cartilaginous endo-skeleton; and in the face, behind the mandible, we find many of the bars ensheathed in their own "ectostoses."

The hyostylic type of skull, which is not seen in the generalised forms, such as *Notidanus* and *Cestracion*, but is common to Skates and ordinary Sharks, is in the "Acipenseridæ" carried to its uttermost pitch of perfection, and here, in this minute larva, recently hatched, and scarcely chondrified, the Selachian type of skull is over-passed, and *at least two* additional segments are seen on each side. These additional joints in the highly subdivided and modified primary hyoid bar are expressly for the purpose of throwing the mouth out far away from the skull; the jaws are suspended on an extremely hypertrophied *upper hyoid segment.*

This hypertrophy of the "epi-hyal" segment is correlated with the atrophy of the uppermost, or suspensorial part of the pier of the mandible, which pier, even in this early larva, is *below the middle* of the hyoid arch Plate (13, fig. 6, *pg.q.*, *mn.*, *hm.*, *c.hy.*).

This is the more remarkable in a type that might have been expected to show something primitive in its visceral arches, seeing that it is only a *Chondrosteus Ganoid*, with a huge, permanently undivided notochord, and a totally unossified chondrocranium.

Even in the Salmon (Phil. Trans., 1873, Plates 1–3), the embryos of which are much larger and more tractable, I did find, *as cartilage*, the primitive facial bars; and their metamorphosis into the highly modified hyostylic type could be traced step by step; but this cannot be done in *Acipenser* nor in *Lepidosteus* (my next subject). In *Scyllium* (Zool. Trans., vol. x., plate 34) this was also possible; but in the Skates, *Raia* and *Pristiurus* (ibid., plates 35 and 39) the earliest tracts of true hyaline cartilage were, already, half metamorphosed, for all the *uppermost* segments (ibid., plate 35, fig. 4) were developed as distinct cartilages, although the remainder of each arch was continuous, and its segmentation could be traced afterwards.*

Here, in *Acipenser*, whilst the cartilage is still very soft, the segments of the highly subdivided hyoid arch are all apparent, although the branchial arches are continuous tracts (Plate 13, fig. 6); but their "pharyngo-branchial" segment—so very distinct in the embryo of the Skate—is already half severed from the main bar (Plate 13, fig. 4, *p.br.*, *e.br.*).

The pier of the mandibular arch, instead of growing up to the basis cranii, is a falcate cartilage (the pterygo-quadrate, *pg.q.*), which lies half-way down the face, and passes forwards and downwards. It is flat, obliquely-placed, and somewhat uncinate in front; behind, it is thick and rounded, and forms a condyle which lies in the concavity of its own lower segment, the mandible (*mn.*). This segment is thick behind; in front of its condyloid depression it sends upwards a coronoid swelling, whilst, behind, it ends in a rounded angular process. The rest of the bar is rounded; it lessens towards its ventral end, and is curved the opposite way to the pterygo-quadrate.

The rounded quadrate region of the upper bar is attached by ligamentous fibres to the lower end of the hyoid pier; that pier is the hyomandibular (*hm.*), the lower, rounded end of which is being segmented off as the symplectic (*sy.*). The whole bar is a massive phalangiform cartilage, gently bent backwards, altogether running downwards and a little forwards, and articulated above by an oblong condyle, to the "tegmen tympani" of the ear-capsule, under the horizontal canal (*h.s.c.*). It is one-third larger than the pterygo-quadrate, but its own lower piece, the cerato-hyal, is somewhat less than the mandibular pier.

* In Selachians themselves, the best of all Fishes in which to study the development of these parts, it is next to impossible to maintain a consistent nomenclature of the elements of the visceral arches. In the Dog-fish (*Scyllium*, ibid., plates 37, 38) the hyomandibular is evidently the serial homologue of the epi-branchials; in the Skate (*Pristiurus*, ibid., plate 35) the uppermost part of all the arches is developed as a separate nucleus of cartilage, and the metapterygoid and hyomandibular naturally classify themselves with the succeeding pharyngo-branchials. Again, the subdivided hyoid pier of *Acipenser*, which also carries the mandibular apparatus, is not divided into a normal pharyngo- and epi-hyal, but the epi-hyal, apparently, is itself subdivided, and there is no pharyngo-hyal.

The cerato-hyal element is a flattish rod, pinched in the middle, and dilated at both ends; its upper end is articulated to the postero-inferior face of the rudimentary symplectic by means of a small intercalary nucleus of cartilage—the inter-hyal (*i.hy.*). The lower end of the bar is nearly segmented off as a short semi-oval hypo-hyal (*h.hy.*). The branchial arches (*br.*) are about half the size of the hyoid—supposing it to have been in one large bar; there are *five* of them, and they decrease in size from before, backwards. The top of each is semi-distinct from the rest as a pharyngo-branchial (*p.br.*); that part is turned inwards, the rest of the arch is curved outwards, and turns inwards and forwards, below, where it joins the basi-branchial bar (Plate 13, fig. 4, *b.br.*).

Second Stage (continued).—*Transversely-vertical and vertical sections of the head of a larva of* Acipenser ruthenus, $9\frac{1}{2}$ *millims. in length.*

The transverse sections (Plate 12, figs. 1–3, and Plate 13, figs. 1–5) will further illustrate the structure of the visceral arches, and also show the state of the basis-cranii at this stage.

Section 1.—The first section (Plate 12, fig. 10) is through the fore-brain (C^1.), and the fore part of the mid-brain (C^2.), the eye-balls (*e.*), and the barbels (*bb.*); here the only cartilaginous tracts are the trabeculæ (*tr.*), which are sub-oval in section, obliquely placed, and separated by a distance equal to their own width; they are sub-concave on their upper surface, where they lie under the thalamencephalon as it narrows to the infundibulum.

Section 2.—The rounded ends of the trabeculæ are free for a very short distance in the extremely short head of this larva, which has at present no rudiment of the huge pre-cranial rostrum afterwards to be developed. In this section (Plate 12, fig. 11) the trabeculæ are wider, flatter, and are in close contact with each other; they lie here under the infundibulum (C^1.) which is covered now directly by the mid-brain (C^2.). Here the fore part of the oral cavity is cut through, so that the front row of teeth (*t.*) are seen, and on each side the outer barbels (*bb.*) are just in view; this section is behind the eye-ball. Above the mouth two oval masses of cartilage, more solid than the trabeculæ, are seen; these are the pterygo-quadrate bars (*pg.q.*) at their fore end.

Section 3.—The next (Plate 12, fig. 12) is close in front of the auditory capsules, through the widest part of the mid-brain (C^2.) where it joins the hind-brain, in the middle of the mouth, and the huge Gasserian ganglia (V.), whose cerebral roots are brought into view. Here the trabeculæ (*tr.*) are in close contact, are wider than in the last section, and they curve well round the base of the hind part of the infundibulum (*inf.*).

Here the pterygo-quadrate cartilages (*pg.q.*) are very solid and curved, and have a sharp edge lying over the "adductor mandibulæ" muscle (*ad.m.*), (see also SALENSKY, *op. cit.*, plate 18, fig. 165, *ad.m.*); these muscles lie outside the concave face of these oblique cartilages; the front teeth and lip are still seen. Above the front face of the auditory capsules (here, by mistake, lettered *e*), the auditory involutions (*aq.v.*) are seen.

Section 4.—The next slice (Plate 13, fig. 1) contains the hinder half of the auditory involution (*aq.v.*), and below it the auditory capsule (*au.*) is seen, in the region of the anterior canal; there is some cartilage in the infero-lateral part of the wall of the capsule. This is behind the mid-brain, and the hind-brain (see figs. 1–3, C^3.) is very large; large masses of ganglionic cells are seen belonging to the 5th, 7th, and 8th nerves (V., VII., VIII.). Outside, the lip of the spiracle (cl^1.) is cut through, and below the brain the large notochord (*nc.*) is shown near its apex. This lies in and between the moieties of the investing mass (*iv.*), which are nearly square—just a little hollow above, and convex below. Below these parts the oral cavity is laid open; right and left of it the thinner hind part of the pterygo-quadrate (*pg.q.*) is severed, and, below, the teeth of the lower lip (*t.*, *l.l.*).

Section 5.—Here the hinder part of the ganglionic mass belonging to the 7th and 8th nerves (Plate 13, fig. 2, VII., VIII.), and some fibres of their cerebral roots are cut through; the spiracle ($cl^{1\prime}$.) is here laid open; above it a cartilaginous tract of the auditory wall is seen. The anterior and horizontal canals, and the vestibule (*a.s.c.*, *h.s.c.*, *vb.*) are laid open. The notochord (*nc.*) is enlarging, and is being enclosed in the square moieties of the investing mass (*iv.*) which lie somewhat under it. Below the mouth the mandibles (*mk.*) are laid bare throughout their entire length, on account of their almost directly transverse position, and over their articular hollow the articular knob (*q.*) of the pterygo-quadrate cartilage is shown *in situ*. The back of the lower lip (*l.l.*) is seen, whose toothed front face was shown in the last section.

Section 6.—Here, on each side of the narrowing hind-brain (Plate 13, fig. 3, C^3.), the auditory capsules are cut through in their widest part, and both the arch and ampulla of the posterior canal (*p.s.c.*) are cut and laid open, as well as the deep saccular part of the vestibule (*vb.*). The infero-lateral shell of auditory cartilage is joining itself on to the more thin and outspread part of the investing mass (*iv.*—line too high); the notochord (*nc.*) is placed directly above the moieties of cartilage. The pharyngeal cavity is here very large, and in its walls we see the large, massive, arcuate epi-hyal element, undergoing segmentation into a long hyo-mandibular and a short symplectic piece (*hm.*, *sy.*). Here the directly transverse position of the parts gives, in one section, the whole of the hyoid series, for the symplectic is seen to be followed, lower down, by the little inter-hyal (*i.hy.*), and that by the long cerato-hyal (*c.hy.*), which is giving off from its sub-triangular end the short hypo-hyal (*h.hy.*). This is the front face of the section, and behind and within the hyoid we see the lower half of the first branchial arch and the fore part of the basi-branchial bar ($c.br^1$.); the branchial arch, like the hyoid, is becoming subdivided below, to form the hypo-branchial. The front part of the ganglionic mass of cells for the 9th and 10th nerves (IX., X.) is cut across.

Section 7.—These most successful and illustrative sections* display all that is sought for; here (Plate 13, fig. 4), on each side of the narrowing hind-brain (C^3.), the

* The sections were made by my son Mr. W. N. PARKER.

notochord has become suddenly twice as wide as in the last, and it has now gained a lower position ; the investing mass (*iv.*) is horn-shaped in section, and the base of each "horn" sits on the supero-lateral face of the huge notochord. The back wall of the auditory capsule (*au.*) is cartilaginous, and at this part is some distance from the basal plate (*iv.*) ; in that interspace the ganglion of the vagus (X.) is shown.

Here, happily, another visceral arch, the second branchial (*p.br.*, *e.br*^{2}., *c.br*^{2}., *b.br.*) is exposed in one slice ; the segments are only indicated by the crowding of cells at the line where segmentation will take place. Within and behind the second branchial arch the third (*c.br*^{3}.) is partly seen, and the large, simple gills (*g.*) are shown fringing the folds of the section, below ; they are clavate, because of the loop of the simple capillary vessel within.

Section 8.—Behind the ear-capsules the notochord has a diameter only two-fifths less than that of the hind-brain (Plate 13, fig. 5, *nc.*, C^3.) ; the investing mass (*iv.*) embraces it more below, and is rising, right and left, so as to form the lower half of the occipital arch (*e.o.*). Behind the gills, under the narrowed pharynx, the yolk-mass is now seen.

A vertical section of the head in one of the larger larvæ of this stage ($9\frac{1}{2}$ millims. long ; Plate 14, fig. 1) shows the low position of all the parts of the fore-brain (C^1., C^{1a}., *inf.*), the forward position of the mid-brain (C^2.) and the huge size of the hind-brain (C^3.). The cavity of the fold of the mid-brain runs equally forwards and upwards, and the infundibulum (*inf.*) looks backwards and is quite distinct from the pituitary rudiment (*py*). The notochord (*nc.*) nearly reaches the latter, it is very large, arcuate, and bent downwards in front, showing no disposition to enter the fold of the mid-brain in the "post-clinoid" region. Two of the barbels (*bb.*) are seen to the right of the mid-line, and behind these we see the thick upper lip (*u.l.*) bounding the mouth (*m.*), which opens directly below the pituitary rudiment. It is a rather narrow passage, and has in its hinder boundary the thick lower lip (*l.l.*) ; in this the mandible (*mk.*) is seen at its ventral end, and the fore end of the pterygo-quadrate cartilage (*pg.q.*) is seen in the upper lip ; these cartilages lie a little to the right of the section, which is exactly in the middle. In the pharynx, above and behind the oral chink, the first three clefts (*cl*$^{1-3}$.) come into view, below these part of the yolk (*y.*), and in front of the yolk the heart (*h.*).

Third Stage.—Larvæ of Acipenser ruthenus *from $13\frac{1}{2}$ millims. to $14\frac{1}{2}$ millims. in total length.*

Amongst the more advanced larvæ of this Fish only one reached the length of $14\frac{1}{2}$ millims., or $\frac{7}{12}$ of an inch ; the next in size were 1 millim. shorter. One of these latter was made into horizontal sections, and others were *dissected* ; the unique specimen was made into vertically-transverse sections.

The external appearance of these, next in size to the last, viz., $13\frac{1}{2}$ millims., is extremely Selachian (Plate 12, fig. 9, and Plate 13, figs. 8, 9). The tail is more than

two-fifths of the whole length, the long arched notochord is ascending towards the upper part of the continuous azygous crest, and three-fifths of the caudal part of the vertical fin, above and below, is being marked off, ready to form the proper heterocercal tail-fin; the narrow crest above develops the "fulcra," and the wider part below the emarginate lobe. The high crest in front of the constriction becomes the backwardly-placed dorsal fin, and the deep crest, below, the anal fin; the ventral fins (*v.f.*) have a rudiment on each side as a thickening of the mesoblast of the abdominal wall close in front of the vent (*an.*); the pectoral fins (*p.f.*) are large and reniform. The region of the stomach still contains enough yolk to give it a swollen appearance; the intestinal region (*in.*) is narrow. The regions of the brain are still clearly seen from the outside; the eye ball (*e.*) is nearly perfect; the auditory capsules (*au.*) are seen as relatively small oval swellings.

The nasal capsules (*ol.*) have their opening almost subdivided into two by the descending flap. The suborbital fold of the face over the barbels is now large, and they (*bb.*) are long and finger-like. The lips (*u.l.*, *l.l.*) are now thick and rounded; the upper is emarginate in the middle, and the lower has a medium lobe; the teeth (*t.*) are now inside the lips. The spiracle is now a very small triangular hole under the auditory capsule (Plate 12, fig. 9, cl^1.); the operculum (*op.*) although very large and extensive does not cover the copious growth of young gills.

Dissections of the cranio-facial skeleton of a specimen $13\frac{1}{2}$ millims. long show, already, a well chondrified framework. The basis cranii, as seen from above (Plate 14, fig. 4), shows a structure very similar to that of an embryo of *Scyllium canicula* $1\frac{1}{3}$ inch long (see Zool. Trans., vol. x., plate 35, fig. 6), or more than twice as long as this embryo Sterlet.

The cartilage investing the notochord (Plate 14, fig. 4, *iv.*, *nc.*) is continued from the spinal into the cranial region with scarcely any change of form and consistence, a state of things quite like what I have found in the Selachians (*op. cit.*, plate 35, figs. 3, 5). In my preparation four pairs of spinal nerves were seen emerging behind the glosso-pharyngeal and vagus (Plate 14, fig. 4, $sp.n^{1-4}$., X., IX.). The bands of cartilage, whose size and form will be further shown in the sections (Plates 14 and 15) are confluent above for a short distance with the auditory capsules (*iv.*, *au.*) close behind the post-auditory nerves (IX., X.). In front of these conjugations there is a large open space, the "meatus internus" (VIII.), between the cartilage of the capsule and that of the skull floor; the latter widens a little in front of the meatus, then narrows a little to form the inner margin of the foramen ovale; outside this notch we see the huge Gasserian ganglion (V.). The investing mass then widens a little, and ascends a little; this wider ascending part is the "posterior clinoid" wall (*p.cl.*), and in it the notochord ends as a small rounded knob.

As in *Scyllium* (*op. cit.*, plate 35, fig. 6) the bands of cartilage then dip considerably, and these prochordal continuations (*tr.*) of the parachordal tracts, are wider than the roots they spring from. Instead of being wide apart, as in the Salmon, in *Lepi-*

dosteus, and in many types, they are really continuous under the pituitary body, as in *Scyllium* and *Raia*, forming a complete floor to the skull for some distance in front of the notochord and the post-clinoid wall; but this part has a small fontanelle immediately below the pituitary body (see fig. 1, *py.*). Opposite the optic nerves they part for a short distance, nearly meet again, and then diverge as two very short out-turned horns, the tips of which are the rudiments of the cornua trabeculæ (*c.tr.*). Between the Gasserian ganglion and the optic nerve (V., *e.*) the trabeculæ grow upwards, forming the rudiment of the alisphenoid (*al.s.*); the walls and roof, however, will be best studied in the sections.

In front of the eye-balls (*e.*), between them and the olfactory sacs (*ol.*), there is a definite antorbital cartilage growing outwards and a little forwards from the trabeculæ; this is the ethmo-palatine (*e.pa.*), a familiar element, which, here, is only semi-segmented from the trabecula. In Skates, as in Urodeles and Teleostei, it is distinct; but in Batrachia and Sharks it is not; it is well seen as a "process" in *Notidanus* (*Heptanchus* and *Hexanchus*, see GEGENBAUR'S 'Selachians,' plate 1, and also in embryos of *Scyllium*, T. Z. S., vol. 10, plate 37, fig. 1, *a.o.*). Here, it helps to form the back wall of the crypt in which the olfactory sac (*ol.*) is lodged; in these Fishes, as in *Lepidosteus* and the Teleostei, there is no distinct "paraneural" cartilage for the nasal pouch.

Leaving the walls and roof of the skull, until I come to the sections, I shall now describe the visceral arches, which are greatly developed since the last stage.

In a side view of these parts (Plate 13, fig. 11) I have shown the arches relative to the other cephalic structures, which are left in outline to give prominence to the view of the arches themselves.

In another figure (Plate 13, fig. 12) the arches are shown as seen from above, and in a third (Plate 14, fig. 5) they are shown as seen from below. The hyoid arch is twice as large as the others, and has undergone most segmentation and specialization; the branchial arches decrease in size and in the amount of their segmentation, from before, backwards.

The proper pedicle of the mandibular arch, in this extremely *hyostylic* type, is not only absent, but the stunted and forwardly projecting "pier" is much further from the normal point of attachment—under the outgoing fifth nerve—than in any of the Selachians. Each of these pterygo-quadrate bars (*py.q.*) is a curved plate of cartilage, thick and bent forwards in its articular region, where it grows out over the temporal muscle, somewhat, to form the rudiment of the "orbitar process," and flat as it widens out in its pterygoid region.

The right and left plates meet each other for some distance in front, a notch separating their round ends; they are gently convex, above, and gently concave, below. These bars reach as far forwards as the antorbital region, but are embedded in the very loosely attached palatal skin, and are thus only slightly connected with the basis cranii. In the angle formed by their convergence a pyriform wedge of somewhat

newer cartilage (*mt.pg'.*) has made its appearance since the last stage; this is, as far as I know, an unique structure, and but for this stage I should have suspected that this keystone piece had been formed by the fusion of a right and left nucleus of cartilage. Others form round it afterwards, but this is the first, as it is also the most important, morphologically, of the pieces that form the *hind palate* of the Sturgeon.

It would not have been difficult to have dealt with the paired pieces that appear afterwards (Plate 16, figs. 5 and 6), as they are manifestly the counterparts of the single or multiple "metapterygoid" cartilages of the Rays. In *Torpedo* (GEGENBAUR'S 'Selachians,' plate 13, fig. 3, and plate 20, fig. 1, Kr., *a*, *b*,*) there are four of these cartilages on each side, but as a rule there is only one in that group, where it is a true metapterygoid segment of the pier, and not a mere "ray," as in the Shark. In Carinate Birds, where the skeleton reaches the utmost limits of specialization, remnants of Ichthyopsidan palatal cartilages reappear—ethmo-palatine, post-palatine, &c.; and in the Woodpeckers ("Picidæ") the palatine membrane bones are joined together under the basis cranii by an ossified cartilage, the medio-palatine (Trans. Linn. Soc., second series, "Zoology," vol. i., plates 1–5).*

MÜLLER simply calls the whole *compound* plate of the adult *Acipenser ruthenus* (*op. cit.*, plate 9, fig. 71, A, B) "unpaariger Gaumenknorpel," and the pterygo-quadrate bars "paariger Gaumenknorpel," so that the interpretation of these parts is left open. I shall merely, for the present, classify this plate with the free cartilages of the "Raiidæ," and call the median piece the "azygous metapterygoid" (*mt.pg'.*); the later pieces, right and left, will simply be called "paired metapterygoid segments" (*mt.pg''.*). In the adult (Plate 18, fig. 4) Mr. HOWES finds a row of four more much smaller segments along the mid line, in front of the main piece.†

The mandibles (*mn.*, *mk.*) are about as long as the upper bars, but after forming a shallow articular cavity on their thick upper end they become rounded rods, and their position is almost transverse, as these dissections, and the transverse sections (Plate 15, fig. 3, *mk.*) demonstrate; they do not quite meet in the middle, at present.

The hyoid arch has five segments in it on each side, but, like the mandible, no basal segment below. The uppermost piece, the hyomandibular (Plate 13, figs. 11, 12, *hm.*) is by far the largest element in the whole series of arches; above, it is articulated by an oval condyle to the under surface of the pterotic ridge, under the horizontal canal ("tegmen tympani"), and below by a cylindroidal condyle to the symplectic (*sy.*).

* The median cartilage seen in the "Myxinoids" (MÜLLER, 'Myxinoids," plate 3, figs. 2–5, U), the "Gaumenplatte"—which partially unites with the trabeculæ in the adult *Bdellostoma* and *Myxine*, and *early* and *totally* in *Petromyzon*, is not part of the palate, as MÜLLER's term would suggest, and as I once thought, but is, as Mr. BALFOUR showed me, the "intertrabecula"—*i.e.*, its hinder or interorbital part.

† In the scanty living remnants of the "Chondrosteous Ganoids," only the "Acipenseridæ" show this peculiar structure; the "Polyodontidæ" show no trace of it (see MÜLLER's 'Myxinoids,' plate 5, fig. 7, there called *Planirostra edentula;* TRAQUAIR, 'Ganoid Fishes of the British Carboniferous Formations,' Part I., "Palæoniscidæ," Palæont. Soc., 1877, plate 7, fig. 1; and BRIDGE, "On *Polyodon folium*," Phil. Trans., 1878, Part II., Plates 55–57, pp. 683–733.

Its form is like that of a phalangeal segment, it is curved backwards, gently, and has an enlargement there, above the middle, the rudiment of the "opercular process." Its axis is coincident with that of the symplectic and the mandible (*sy.*, *mn.*, *mk.*), together they form a crescentic series, passing downwards and gently forwards, and having the convex margin behind; they are bent inwards below (fig. 12). The curve forward, as well as downward, brings the lower end of the symplectic under the pituitary body; this cartilage (*sy.*) is only one-fourth the length of the upper piece (*hm.*), but it is as thick as its thickest part; it is scooped above for the hyomandibular, and rounded below, where it is tied, by ligaments, to the two elements of the first arch (*pg.q.*, *mn.*, *mk.*).

In the Teleostei the inter-hyal is articulated to the inside of the non-segmented cartilage uniting the hyo-mandibular and the symplectic; in the Sturgeon it is articulated to the inside of the distinct symplectic, rather below the middle—at least at this stage (Plate 13, fig. 11, *i.hy.*). The inter-hyal is a small piece of cartilage, wedge-shaped, with its narrow end upwards; its broad lower end articulates with the top of the cerato-hyal, which is bilobate above, the inter-hyal articulating with the larger upper lobe (fig. 12, *i.hy.*, *c.hy.*).

The cerato-hyal is a thickish, somewhat sigmoid bar, it passes inwards and forwards and nearly meets its fellow of the opposite side; there is no basi-hyal, but a semi-oval segment is formed out of the ventral end of each cerato-hyal; this is the hypo-hyal (*h.hy.*).

The branchial arches (Plate 13, figs. 11, 12, and Plate 14, fig. 5) are larger than the lower part of the hyoid at first, but they lessen backwards, so that the last is only one-fourth as solid as the first. The first three develop a hypo-branchial segment (*h.br.*) exactly like the hypo-hyal, but larger. The inturned dorsal end of all but the last is segmented off as an epi-branchial (*e.br.*), and its apex becomes distinct as a small pharyngo-branchial (*p.br.*) in the first four arches.

The basi-branchial (*b.br.*) is a thickish rod, rounded in front and compressed behind; it only carries the first three arches; the fourth and fifth meet below.

Bony scutes are now developing in the skin, and in the skin of the mouth and the mucous membrane of the palate and fauces several bony plates have appeared; all these are determinable.

In the upper and lower views (Plate 13, fig. 12, and Plate 14, fig. 5) these plates, *most of which are dentigerous*, are shown in their relation to the visceral arches and the largest of these bones; the maxillary and dentary—of one side—are shown separately (Plate 14, fig. 6, *mx.*, *d.*). There is no determinable premaxillary, which like the nasals, and vomers, only exists *as one or many* of a great number of generalised scutes that are to be found in those respective regions. The maxillary (fig. 5, *mx.*) runs across and meets its fellow in front of the pterygo-quadrate (*pg.q.*); it is a long, subarcuate bar, with thickened edges, and carrying five or six sharp, recurved teeth on its anterior third; it is somewhat notched and bent in its hinder third. The dentary (*d.*) is almost

exactly like it, but gently bent in the opposite direction; its teeth look a little forwards and fit in between those of the upper jaw.

The palatine (Plate 14, fig. 5, *pa.*) is a styloid tract of bone binding on the external edge of the broad fore part of the suspensorium (*pg.q.*); it is edentulous. The pterygoid (fig. 5, *pg.*) carries teeth; it is a thin plate of bone, which lies inside the hinder convex edge of the cartilage.

Over the rudimentary "orbitar process" of the suspensorium a small scale of bone is visible, just as when the squamosal is formed over the quadrate in the Amphibia;* this is the preopercular (*p.op.*). In the roof and sides of the pharynx inside the first branchial arch there are three pairs of small, arcuate, dentigerous scales of bone (Plate 13, fig. 12, and Plate 14, fig. 5); these are "upper pharyngeal bones." Clamping the hinder part of the hyomandibular, its rudimentary "opercular process," the opercular bone (*op.*) is seen; it is a convex shell, with spurs in front and a sharp round margin behind. These bones are evidently all mere parostoses; the "ectosteal" sheaths of the visceral arches have not appeared yet; the cranium never acquires any well-grafted bony plates.

Third Stage (continued).—*Horizontal sections of one of the lesser larvæ of* Acipenser ruthenus, *at this stage*—13½ *millims. long.*

Section 1.—The uppermost of these sections (Plate 13, fig. 10) is through the hemispheres and the base of the mid-brain directly over the thalamencephalon (C^{1a}., C^1.), the eye-balls (*e.*), and the front and sides of the mouth (*m.*). The quadrate and pterygoid regions (*q.*, *pg.q.*) are severed, being cut through where there is a depression above; moreover, the broad pterygoid plate is obliquely placed, and thus this horizontal section shows its thickness, but not its breadth. Between the hooked fore ends of these cartilages a newer tract, the lozenge-shaped azygous metapterygoid (figs. 10 and 11, *mt.pg'.*), is seen. Behind the transversely oval quadrate region the lower part of the hyomandibular (*hm.*) is cut across; it is obliquely placed, and between the two sections of cartilage, on the outside, the lower part of the first cleft or spiracle (cl^1.) is laid open. Part of the "adductor mandibulæ" muscle (*ad.m.*) is seen outside the pterygo-quadrate bar, and the opercular fold of the first cleft is seen with its rough inner surface.

Section 2.—The next section, below the last, is through the whole length of the pterygo-quadrate bar (Plate 14, fig. 2, *pg.q.*), which is seen to be of almost uniform thickness, and of a sigmoid shape; the fore end is turned inwards, and the hind part outwards. Behind it the top of the articular region of the transverse mandible (*mk.*) was sliced off. The basis cranii (*tr.*) is cut through close in front of the post-pituitary wall and the notochord, where the trabeculæ are completely confluent; the large infundibulum (*inf.*) is severed at its "neck" (see Plate 14, fig. 1, *inf.*). Here, this process of

* The squamosal of the Amphibia has a large descending *preopercular process;* but there is no separate preopercular bone, such as Fishes possess.

the brain is above and in front of the distinct pituitary body (fig. 1, *py.*), and seems to be distinct from the fore-brain (C^1.); this, however, is due to the manner in which it has been cut through on its projecting part. In this section the rudimentary hemispheres (C^{1a}.) are cut through where they pass forward from the first cerebral vesicle (figs. 1 and 2, C^1., C^{1a}.). The small olfactory sacs (*ol.*) are cut across; they lie outside the junction of the hemispheres with the thalamencephalon; the eye-balls (*e.*) are cut through in the lower part.

Section 3.—The lowest section (Plate 14, fig. 3) is through the lower part of the curved head, and takes in the whole boundary of the mouth (*m.*; see also fig. 1). The olfactory capsules are removed, and the barbels (*bb.*) are cut across at their root; each, at present, contains a pith of true cartilage. The fore part of the pterygo-palatine and the quadrate region of the same (*pg.q.*, *q.*) are shown as severed, and the latter is seen as a transverse process, bulging below to form the hinge of the jaw. Behind the mouth (*m.*) the lower lip is seen with its teeth (*l.l.*, *t.*), and in the substance of this visceral fold the whole length of the mandibles (*mk.*) is shown, first thick, in the articular region, then slenderer, and again enlarging distally.

Third Stage (continued).—*Transversly vertical sections of the head of the largest larva of* Acipenser ruthenus; $14\frac{1}{2}$ *millims. long.*

Section 1.—The first section (Plate 14, fig. 7) is through the barbels (*bb.*) at right angles to the horizontal section just described (fig. 3), and also to the axis of the down-bent brain which is here developed into the rudimentary hemispheres (C^{1a}.). The plane of this section would form an angle of 45° with the plane of a section taken vertically through the hind part of the hind-brain, or through the front of the yolk mass and heart in such a larva as is shown in a longitudinally-vertical section (Plate 14, fig. 1, C^3., *y.*, *h.*). That, however, was a younger larva, and the head in this had straightened a little.

The hemispheres (fig. 7, C^{1a}.) are here shown to be, together, sub-oval in section, somewhat grooved above, and slightly protuberant below. The olfactory sacs (*ol.*) have no roof in front, and their floor is formed by the ethmo-palatine cartilage (*e.pa.*), which is distinct, in front, from the trabecula. The skin of the fore face, however, is developed into a valvular fold around the opening, and the mucous membrane is applied to the rising and falling of the structures that encompass it; there is no proper "paraneural" cartilage over the nasal capsule; in this, *Acipenser* agrees with *Lepidosteus* and the *Teleostei*, and differs from the Selachians, Cyclostomes, and Amphibia. Here the floor (*e.pa.*) is flat and distinct, and there is a considerable space between it and the trabecula (*tr.*) which is thick at its outer edge, and thins out towards its fellow of the opposite side, which it does not quite meet.

Section 2.—The next section (Plate 14, fig. 8) is through the widest part of the hemispheres (C^{1a}.) which are nearly oval in the section, from side to side, the top being convex as well as the bottom; this latter part is, however, narrower than the upper.

Here the roots of the front teeth are cut through in the base of the upper lip (*u.l.*, *t.*), and here the nasal pouch (*ol.*) has both roof and floor; the latter is continuous, now, with the trabecula (*tr.*) and bulges downwards, whilst the roof (*s.ob.*) is the fore end of a large tract of superorbital cartilage, which grows independently of the floor for some distance backwards—a very common thing in the Ichthyopsida.

This upper band is the lateral rudiment of the tegmen cranii, which in this type so soon covers in the great fontanelle and becomes so very massive; at present it is very similar to the palato-trabecular band (*e.pa.*, *tr.*) below; here the trabeculæ are wider apart than in the last section.

Section 3.—In this third pre-oral section (Plate 14, fig. 9) the projecting fore part of the mid-brain is seen to lie on the fore-brain (C^2., C^1.). This is through the back part of the olfactory pouch (*ol.*), which is becoming complicated; its palato-trabecular floor (*e.pa.*, *tr.*) is, here, at its widest and most solid part, and the superorbital roof over the nasal sac is narrower, and is sharp at its outer edge; the roots of the front teeth are still in view (*u.l.*, *t.*).

Section 4.—This is through the fore part of the eye-balls (Plate 14, fig. 10, *e.*); there is, here, a very solid lateral ethmoidal wall uniting the superorbital band and the trabecula (*s.ob.*, *tr.*); the latter is losing its palatine extension, outwards, and the two plates are still a good distance apart beneath the fore-brain (C^1.). Here the antorbital wall is cut through; it is membranous, at present.

Section 5.—In this section (Plate 14, fig. 11) the superorbital band (*s.ob.*) is simply a moiety of the tegmen cranii, for the projecting part is gone, and each band is creeping towards its fellow over the front of the mid-brain (C^2.). So also, below, the trabeculæ (*tr.*) have lost their palatine projection and they are creeping towards each other under the fore-brain (C^1.); these latter are the larger plates, and are rather indented below in the middle. Opposite the eye-ball, the front third of which is cut across, there is a small tract of cartilage cut through; it is rounded above and sharp below; this is a tract which runs backwards as far as to the Gasserian ganglion (see Plate 15, figs. 2, 3, *al.s.*, V.); it is orbito-sphenoidal here (*o.s.*), and alisphenoidal behind.

Section 6.—The lens of the eye (Plate 14, fig. 12, *e.*) is now reached, and the sclerotic is becoming cartilaginous; this section is very similar to the last, but the superorbital and orbito-sphenoidal bands (*s.ob.*, *o.s.*) are thinner, and the trabeculæ (*tr.*) are approximating; here the fold of the upper lip (*u.l.*) is cut through; it is seen to be folded off from the fore face, so that at this point it seems to be attached by a narrow isthmus; the next two figures will explain this (see also Plate 13, fig. 11).

Section 7.—This and the next (Plate 14, figs. 13, 14) are through the highest (or deepest) part of the brain, for here the bulging mid-brain (C^2.) lies right over the fore-brain (C^1.) in front of the infundibulum, which is cut through behind the second of these (Plate 14, fig. 1, *inf.*). Here the growing roof and walls of the orbital region of the skull are composed of *three* bands on each side (*s.ob.*, *o.s.*, *o.s′.*), for over the emerging optic nerve a lower tract of cartilage has appeared, which is thick on its

inner face, growing into the sulcus between the swellings of the brain (C^2., C^1.). Here the large optic foramen is a "fenestra," as in Frogs; its upper margin is formed by this lower orbito-sphenoidal process (*o.s'.*), and its lower edge by the trabecula (*tr.*); this plate now touches its fellow of the opposite side. The upper lip (*u.l.*) is seen in all its depth here, and the teeth (*t.*) are in full view; they are looked at from behind.

Section 8.—In this slice (Plate 14, fig. 14) the hinder half of the eye-ball and optic nerve (*e.*, II.) is seen, and the brain (C^1., C^2.) is here at its greatest bulk. The trabeculæ (*tr.*) are confluent, are thicker, and rise more at the sides; this is close in front of the post-pituitary wall. The thick hind part of the orbito-sphenoid is now ready to become alisphenoidal; its two parts are molten together, and the upper tract or super-orbital (*s.ob.*) is now thickening as it approaches the auditory sac, ready to become the postfrontal ("sphenotic") wing.

Close behind the upper lip (*u.l.*) two curved plates of cartilage are cut across; these are the pterygo-quadrate bars (*pg.q.*), they are thick outside, and bevelled where they meet.

Section 9.—In this section (Plate 15, fig. 1) the mid-brain (C^2.) is at its widest part and overlies the infundibular end of the fore-brain (*inf.*), to which the pituitary body (*py.*) is becoming attached; this is through the hinder part of the eye-balls (*e.*), and close in front of the Gasserian ganglion (see fig. 2, V.).

The superorbital band is now the "sphenotic" (*sp.o.*); below it there is a large membranous fenestra, and the short oval section of the narrow alisphenoidal band (*al.s.*). The trabeculæ (*tr.*) are apart again, where the pituitary body (*py.*) passes down; they are altogether narrower here, and are grooved by vessels below. Here the pterygo-quadrates (*pg.q.*) are cut through their middle part, and here, in the re-entering angle behind their upper junction, a considerable wedge of cartilage is seen; this is the azygous metapterygoid (*mt.pg'.*); it has a pair of smaller pieces (*mt.pg''.*) or lateral metapterygoids attached to it; underneath this arched palate a number of teeth (pterygoid teeth) are seen.

Section 10.—This section (Plate 15, fig. 2) escapes both the eye-balls and ear-sacs, and is through the body of the Gasserian ganglion (V.) and behind the pituitary body. Here the trabeculæ are confluent again in front of the low post-pituitary wall and the end of the notochord. The sphenotic cartilage (*sp.o.*) is now ear-shaped in section, convex outside, and has two sub-concave inner faces, one applied to the skull-wall and one hanging down free. The pterygo-quadrates (*pg.q.*) are cut across a little in front of the hinge of the lower jaw, they are acuminate-oval in section, with the point downwards. The lower lip with its teeth (*l.l.*, *t.*) is here displayed, and the large "adductor mandibulæ" (*ad.m.*) is cut across its belly.

Section 11.—This (Plate 15, fig. 3) is the first of the auditory sections; the capsules (*au.*) are severed in their antero-superior-angle, to which is attached the upper and lower processes of the sphenotic (*sp.o.*). Through the wall of the capsules the ampulla of the anterior canal (*a.s.c.*) is seen. The alisphenoid (*al.s.*) re-appears in this

section, and is twice as large as in fig. 1; the Gasserian ganglion (V.) is here cut through behind, and lies within its proper boundaries, namely, with the alisphenoid (*al.s.*) above and the investing mass (*iv.*) below. This section is near the edge of the low post-clinoid wall (Plate 14, fig. 4, *p.cl.*) and the apex of the notochord (*nc.*), which here lies on the gently-scooped plate formed by fusion of the two parachordal bands (*iv.*). The pterygo-quadrate (*pg.q.*, *q.*) is cut across close in front of the hinge, above and below, for it appears in two parts on account of its curve downwards to form the hinge. MECKEL's cartilages also (*mk.*) are cut through close to the hinge; they are placed across, behind the mouth, are gently arcuate, and slowly lessen towards the meeting point. Outside the hinge, an angle of the symplectic (*sy.*) has been cut off.

Section 12.—This section, half of which was drawn (Plate 15, fig. 4) like the last, is a *front view;* here the cavity of the auditory capsule is laid open, with the ampulla and part of the arch of the anterior semicircular canal (*a.s.c.*). The sphenotic cartilage is still seen above and below this front part of the capsule; from the capsule to the investing mass is the foramen ovale with the ganglion of the 5th (V.), perhaps also part of the "ganglion geniculatum," which belongs to the facial and auditory nerves (Plate 14, fig. 4. VII., VIII.); the notochord (*nc.*) still lies on the investing mass (*iv.*). The hinge of the lower jaw is seen from its front face; the rod of the mandible (*mk.*) was in the last section, and this shows the articular region. The quadrate end of the pterygo-quadrate (*q.c.*) is seen in its full size with its orbitar process (*or.p.*); outside the hinge the symplectic (*sy.*) is shown, and the hypo-hyal and half the cerato-hyal (*h.hy.*, *c.hy.*), and some of the teeth of the lower lip (*t.*), towards the mid line.

Section 13.—In this section (Plate 15, fig. 5) the hind-brain (C^3.) is becoming narrower, and each auditory capsule under the arch of the anterior canal (*a.s.c.*), is cut through so as to expose the ampulla of the horizontal canal (*h.s.c.*); above, there is a rudimentary tegmen cranii, continuous with the capsule and the hind part of the "sphenotic" tract. At this part the capsule, as is the rule in Fishes, is open towards the hind-brain, and in the fissure, below, the "ganglion geniculatum" (VII., VIII.) is shown. Here the capsules and the basal plates (*iv.*) are quite confluent, and the notochord (*nc.*) divides the latter, lying down between the two halves. The front face of this section was figured; here the massive symplectic (*sy.*) is shown in its front half, and a considerable portion of the cerato-hyal (*c.hy.*); the hypo-hyals are lost in this section, they were shown in the last (fig. 4); the basi-branchial, the first hypo-branchials, and part of the first cerato-branchials ($h.br^1$., $c.br^1$.) are shown here as well as the "protractor hyomandibularis" muscle (*pt.*, *hm.*). Teeth (*t.*) are seen as far down, inside the throat, as the first hypo-branchials.

Section 14.—In this section (Plate 15, fig. 6), the hind-brain (C^3.) is much smaller, but the auditory capsules are at their widest part; they are continuous with the thickening parachordals, which enclose an enlarging notochord (*iv.*, *nc.*). Below these parts and their underlying vessels, teeth (*t.*) are still seen. The super-occipital tegmen (*s.o.*) is growing inwards from the edge of the capsules, but these margins of the great fontanelle are nowhere closed in (from end to end) at present.

The arch of the anterior and horizontal canals, and the vestibule (*a.s.c*, *h.s.c.*, *vb.*) are laid open, and below, in the great open "meatus internus," the ganglion of the 7th and 8th nerves is still seen.

The hyomandibular (*hm.*) is here articulated by its convex head with the concave surface of the auditory capsule, and looks like the proximal segment of a large limb joined to its own limb-girdle. This is correlated with the downgrowth of the mouth, whose own arch has been carried far away from its cranial attachment. Here we see the symplectic, inter-hyal, and proximal part of the cerato-hyal (*sy.*, *i.hy.*, *c.hy.*); and behind these, near the middle, the lower part of the first and second branchial arches ($h.br^1.$, $c.br.^2$, $h.br^2.$, *b.br.*).

Section 15.—In this section (Plate 15, fig. 7) the posterior canal (*p.s.c.*) is laid open throughout its whole extent, and here the capsule (*au.*) is re-acquiring an inner wall. Below, it is joined to a very solid basal plate (*iv.*), right and left, the moieties of this plate clip the large notochord (*nc.*), which is only partly embraced by them.

Parts of the first and second branchial arches ($p.br^1.$, $e.br^1.$, $c.br^1.$, $c.br^2.$) and some gill papillæ come into view here.

Section 16.—In this view (Plate 15, fig. 8) the back wall of the auditory capsule (*au.*) behind the posterior canal is shown; here the massive basal plates (*iv.*) are growing upwards to form the occipital arch (*e.o.*), and are separated from the auditory capsules by a large chink. Here the 9th and 10th nerves (IX., X.) are seen growing from the hind-brain ($C^3.$), forming their ganglia and giving off their trunks. Part of the gill arches (*br.*) and their gills are shown on each side of the pharynx.

Section 17.—Here we see (Plate 15, fig. 9) that the occipital arch (*e.o.*) is imperfect above; below, each mass of cartilage (*iv.*) cleaves closely to the huge notochord (*nc.*) the arch is produced into the angular processes on each side that project from the auditory capsules (see fig. 13).

Fourth Stage.—Young Sturgeons (Acipenser sturio), $7\frac{1}{4}$ *to* 8 *inches long.*

In this stage the Fish is completely metamorphosed, and the only important change which takes place afterwards is immense increase in size, and the addition of certain bony centres, both parosteal and ectosteal.

I have had no intermediate sizes between *Sterlets* 7 lines long and *Sturgeons* 7 inches long, but in *Lepidosteus*, another Ganoid (the subject of my next paper), two instructive stages come in at this point, and make the interpretation of this lower type of skull easy.

In larval *Lepidostei* the size of my largest larval Sterlets, namely, about 15 millims., the azygous intertrabecula has already filled in the space between the trabeculæ, in front; and in specimens already like the adult, and 1 inch long, the trabeculæ have developed their cornua, and the intertrabecula has shot forwards as a long pre-cornual rostrum. At that stage the endocranium of *Lepidosteus* is extremely Acipenserine, and explains, and is explained by, the skull of this stage in the young Sturgeon.

A. *Ectocranium of the young Sturgeon* (Acipenser sturio).

In this stage there are scarcely any proper "parostoses" and very few "endostoses," but the head is well covered with "dermostoses" that are simply the ordinary Ganoid scutes (Plate 15, figs. 10–12), brought more or less into relation, both in *form* and in *number*, with the underlying endo-skeletal structures.

Of course, the homology of these scarcely altered superficial scutes with the special deep laminæ of bone that are so completely dominated by the endocranium in higher types, is imperfect and partial. These scutes present us with *too much* or *too little* when we are looking for the normal, highly specialised "investing bones" of the higher types; their inner layer, only, can correspond with those bones, and that is but imperfectly related to the parts within. Moreover, it is only in certain regions that any strict comparison can be made: this is in those cases where some unusually large scute has starved out its neighbours and has become the roof or wall of some particular part of the skull or face. Nevertheless, for the sake of uniformity of language, I shall call that scute which more perfectly than any other covers the nasal capsule, the *nasal* (*n'*.); the large plates over the hemispheres, the *frontals* (*f'*.); those over the mid-brain, the *parietals* (*p'*.); and those over the auditory ledge, the *squamosals* (*sq'*.).

In the face it will not be difficult to seize upon the true meaning of certain ichthyic bones, namely, the "operculars;" and the "splints" (parostoses) that are applied to the highly specialised pterygo-quadrate and mandibular apparatus will also, by comparison with like parts in other Ganoids, and in the *Teleostei*, be interpretable.

The round swollen head of the larva (Plate 12) is now changed into a long wedge-shaped recurved rostral structure (Plate 15, figs. 10–12), and this structure is invested now by solid ganoid plates in great number; but only certain of these can be pitched upon as deserving a special name.* The number of bones covering the snout is very great; none of these can be called "premaxillary," only one can even by courtesy be called "nasal" (figs. 10, 11, *n'*.), whilst below (fig. 12) several bones contend for the name of "vomer." The eye is protected by supra-, post-, and sub-orbitals (*s.ob.*, *pt.ob.*, *su.ob.*); the post-orbitals run back and become temporal scutes, the chief of which is called the squamosal (*sq'*.). A very fine scute lies over the opercular region and is the true opercular (*op.*); under it there are two rugged, squarish plates—these are the sub-opercular and inter-opercular (*s.op.*, *i.op.*); the pre-opercular (Plate 16, fig. 1, *p.op.*), as in *Lepidosteus*, is a very small "parostosis," applied to the side of the quadrate region of the suspensorium.

The orbital rim and eye (fig. 10) are small; the nasal pouch has a small upper, and a large lower opening; these openings are obliquely placed, so that the upper is also the foremost space. These capsules keep close to the antorbital region; in *Lepidosteus* they are carried to the end of the long beak. Behind the main post-orbital, and at

* I must refer my readers to the views of those excellent "experts" whose works are referred to in the Bibliographical List, especially to those of Professors Huxley, Traquair, and Bridge.

the antero-superior angle of the opercular, the small spiracle (cl^1.) is seen ; inside the opercular the *half*-gill of the hyoid arch may be seen, transferred from its own arch, now required for suspensory purposes, and attached to the inner face of a specialised ganoid scute. The mouth and lips (fig. 12, *m.*, *u.l.*, *l.l.*) are now curiously modified, and this structure is extremely protusible ; the opening is transverse, and crescentic when closed.

The barbels (figs. 10, 12, *bb.*) are long and slender, now ; they have lost their cartilaginous pith.

I shall describe the oral parostoses with the cartilages to which they are attached.

B. *Endocranium of young Sturgeons from* 7¼ *to* 8 *inches long.*

When the superficial bones have been removed we find an extremely solid chondrocranium underneath (Plate 15, fig. 13, and Plate 16, figs. 1–4). In the last stage there was a continuous membranous fontanelle along the whole top of the head, the orbitosphenoidal region was partly membranous, right and left, a small fontanelle existed under the pituitary body, and an open notch in front between the trabeculæ.

Now, the only membranous space is a small trilobate supraoccipital fontanelle (Plate 15, fig. 13, *s.o.*, *fo.*), not over the proper brain cavity but in an extension of the chondrocranium over the fore part of the spinal region.

Everywhere there is the same intense hypertrophy of the hyaline cartilage, and in no part of the cranium, proper, nor in the auditory capsules, do true "ectosteal" plates graft themselves upon the cartilage—even in very old individuals ; moreover there is no *calcification* of the surface-cartilage, such as is seen in the Selachians. Even now, in these young specimens, the actual size of the brain and brain-cavity is extremely small (Plate 16, fig. 2) in proportion to the size of the skull ; which, measured to the end of the rostrum, is three times the length of the cranial cavity.

Here we see the permanence of the early "mesocephalic flexure ;" for besides the sudden loop formed by the mid-brain, represented now by the post-pituitary chink, which looks forwards, the solid ethmoidal region of the skull is bent gently, but steadily, downwards, before it rises to form the recurved rostrum. The orbits are very large, out of all proportion to the small, thick, cartilaginous sclerotics ; the nasal capsules (*ol.*) are set in the sides of the hind part of the huge rostrum, the ethmo-palatine or antorbital wings of which are thick and twice swollen. The rostrum is composed of three tracts, answering to the three offshoots of cartilage that have grown so rapidly since the last stage from the end of the primary chondrocranial floor-bands—the short *prochordal* trabeculæ. Seen from above (Plate 15, fig. 13) and in section (Plate 16, fig. 2, *c.tr.*, *i.tr.*) the rostrum is convex at its edges, and gently concave in the middle ; but below (Plate 16, figs. 3, 4) it is like a sagittate leaf—thick and succulent—with a very solid convex mid-rib and thickened margins ; here the margins are the cornua trabeculæ and the mid-rib the intertrabecula (*c.tr.*, *i.tr.*). The deepest

part of the skull is in the presphenoidal region, close behind the huge aliethmoidal and ethmo-palatine outgrowths ; (compare in Plate 16, figs. 1–4, *al.e.*, *e.pa.*, *tr.*, *i.tr.*).

Here the deep middle part is formed by the hinder intercalating part of the huge intertrabecula (*i.tr.*), and the thick suborbital ledges, close beneath the optic nerves (II.), are expansions of the trabeculæ (*tr.*) behind their cornua (*c.tr.*). In the sectional view (Plate 16, fig. 2) a peninsula of cartilage is almost insulated, below, and the last two of the vomerine series (Plate 16, fig. 3) in front of the fore part of the parasphenoid (*pa.s.*), behind, have crept into the chinks of the cartilaginous mass. A deep, rounded notch, right and left, separates the antorbital from the postorbital (sphenotic) masses of cartilage, which are thick, round, leafy plates turning their convex margin the one to the other (Plate 15, fig. 13 ; and Plate 16, figs. 1, 3, and 4, *al.e.*, *sp.o.*).

Here, again, in front of and around the auditory capsules the cartilage has grown freely, yet not, at present, hiding the form of the imbedded labyrinths in the lateral and upper views (Plate 16, fig. 1, and Plate 15, fig. 13, *a.s.c.*, *h.s.c.*, *p.s.c.*) ; and here, in the midst of all this profusion of cartilage, there is an open "aqueduct" (*aq.v.*) between the anterior and horizontal canals.*

The trilobate fontanelle has a cranio-spinal position (Plate 15, fig. 13, *fo.*), and behind it the cartilage runs, without division, along the spinal roof as a stout rounded process, whilst on each side there is a longer, arcuate, diverging process, growing from the epiotic and pterotic regions; the paired processes reach almost as far back as the branchial arches; they end over the fourth. Even the segmentation of the skull from the spine is absent, as it was in the larva (Plate 14, fig. 4); and the section (Plate 16, fig. 2, *sp.n*$^{1-6}$.) shows the exit of the first six of the spinal nerves.

However we may interpret this continuity of the chondrocranium with the spine, it is a very important thing to note it fairly down. The general form of the chondrocranium as seen from above is like that of two broadly sagittate leaves, set end to end by their broad leaf-stalks—the narrower orbital region ; but the hinder half, as we have seen, is trilobate, and not simple at its free end. The arched canals (Plate 15, fig. 13, *a.s.c.*, *h.s.c.*, *p.s.c.*) are midway between the sphenotic lobes and the roots of the paired cranio-spinal processes (*c.s.p.*), and the small aqueduct opens in the hollow formed by the arches. They project above the large lateral "eave" (Plate 16, fig. 1) ; to the front third of this outer projection the hyomandibular (*hm.*) is articulated by its convex condyle. Looked at laterally, the skull shows the 5th (V.) nerve emerging in front of the hyomandibular, the 7th (VII.) inside it, and the 9th and 10th (IX., X.) further back.

The hind part of the basis cranii is strongly under-floored by the huge parasphenoid (Plate 16, figs. 2 and 3, *pa.s.*), in section (Plate 16, fig. 2) it is only seen as far back as the 2nd spinal nerve, but beneath (Plate 16, fig. 3) its forks are shown to pass far back as to about the 10th; behind the parasphenoid the neuro-central

* This passage, which I find in *Siren lacertina*, has been described and figured in *Polyodon*, by Bridge (Phil. Trans., 1878, Part 2, Plate 56, fig. 5, *f.g.*, *p.f.*, p. 699).

cartilages appear right and left of the notochord. That rod (*nc.*) is invested with a thick mesoblastic sheath of true cartilage, which, as the sections show, is thoroughly confluent with the parachordals in the basis cranii. In front (Plate 16, fig. 2, *nc.*, *p.cl.*, *py.*), it runs up nearly to the pituitary space, but does not ascend into the post-clinoid wall—an arched and almost horizontal plate of cartilage, the *true organic end* of the skeletal axis ; all the rest, to the end of the snout, is formed of special outgrowths from the fore end of the basal plates. The relative size and thickness of the various parts of the chondrocranium will be shown afterwards in the description of the sections.

C. *Visceral arches of a young Sturgeon $7\frac{1}{4}$ inches long.*

There is no *distinct* rudiment of any arch in front of the mandibular, with its extended and complex pterygo-quadrate "pier;" the rudiment of the ethmo-palatine cartilage only exists as an extension of the aliethmoidal mass (Plate 16, fig. 1, *al.e.*). The pterygo-quadrate plate (Plate 16, figs. 1, 4, 5, 6, *pg.q.*) lies in an almost horizontal plane, and at a very variable distance from the basis cranii. The right and left plates meet by their extensive straight upper edge ; then they curve outwards and backwards ; their fore margin is rounded, their inferior edge concave, and their hinder edge is sinuous and notched. Outside the rounded condyle (*q.*) there is a leafy growth, imperfectly adze-shaped, which passes outside the adductor mandibulæ ; this is the "orbitar process" (Plate 16, figs. 1, 7, *or.p.*). Three-fourths of their inner face is invested by the pterygoid bone (*pg.*), a thickish plate with a deep gap in its blade, in front ; the front third of the cartilage is bare, and its hinder margin has suffered absorption—not direct ossification, through the pressure of the pterygoid bone. A sharp style of bone, with its broad end in front, lies along the concave antero-inferior margin ; this is the palatine (*pa.*)—a mere parostosis.

A larger bone curves round the front of each plate, where the two sides meet—both bone and cartilage—and then runs backwards, outside the adductor mandibulæ, and is attached to the outer face of the orbitar process ; this is the maxillary (*mx.*). Mounted on the hind part of the maxillary, and at right angles with it, there is a little triangular bone, with its apex upwards ; it binds against the ribbed outer edge of the quadrate region of the cartilage ; this is the pre-opercular (*p.op.*), smaller, here, than in *Lepidosteus.*

The mandible (*mk.*) is shorter than the forwardly extended pier, it is like that of a Tadpole, having a thick articular region, a hollow for the quadrate, a rounded angular process, and a short terete main rod ; a flat dentary bone (*d.*) invests its outer surface, which has a similar outline to the rod.

The most remarkable part of this apparatus, however, is the *common compound* (tesselated) "metapterygoid" region. At first (Plate 13, fig. 10) the main middle piece, only, was present ; then a right and left segment appeared (Plate 15, fig. 1) ; now (Plate 16, figs. 1, 5, 6, *mt.pg'.*, *mt.pg''.*) there are fifteen. These have a general

symmetry, the large median piece being sub-oval and the large lateral pieces wedge-shaped; but the number of the lesser segments varies, and the outermost, on the left side, is only half separated. In front, the edge is turned downwards (Plate 16, fig. 6), and here a second median cartilage appears, with three lesser segments on the right, and two on the left side. The whole of this "unpaariger Gaumenknorpel" (MÜLLER) is a gently convexo-concave, two-winged structure, which finishes the hard roof of this remarkable tubular protractile mouth.

The uppermost segment of the hyoid arch (*hm.*) is nearly twice the height of the ascending, but arrested, quadrate region; it is the largest of five "internodes" in this double-sized, forked arch, with its double function. The head of the hyomandibular is rounded (Plate 15, fig. 13, and Plate 16, figs. 1, 5, *hm.*); it curves backwards, and sends from its lower two-thirds a large thick flange, the opercular process; this causes the width of the bar to be more than doubled. Its lower condyle is cylindroidal, and the concavity on the next joint answers to it, so that it is like the humero-ulnar joint of a Mammal. Just the neck of the bar is ringed with an *ectosteal* deposit. The next segment, or symplectic (*sy.*), is scarcely half the bulk and length of the last, and its shape is different; it is a phalangiform cartilage, hinged to the hyomandibular, above, tied by ligament to the quadrate and angle of the jaw, antero-inferiorly, and having a little concave facet inside its upper part for the inter-hyal (*i.hy.*), a very small subquadrate segment.

This small *secondary* suspensorium carries the lower part of the arch so that it lies inside the upper; it is composed of two segments, for the distal fifth is segmented off; the main piece is the phalangiform cerato-hyal (Plate 16, figs. 1, 4, 5, *c.hy.*). The middle third is ossified; the distinct piece at the end, the semi-oval hypo-hyal (*h.hy.*), is soft; they meet by their narrow rounded ends, without the intervention of a basi-hyal.

The rest of the arches—the five branchials (Plate 15, fig. 13, and Plate 16, figs. 1, 4, 5) —are very uniform, very solid, grooved on their outer faces for the branchial vessels, and are quite unossified at present, and at present they have only one common basal bar, the basi-branchial (*b.br.*), which does not reach the last arch. They form, below (Plate 16, fig. 4), a very regular series with the lower part of the hyoid arch; they are, in their lower part, larger than the cerato-hyal at first, and then lessen, backwards.

Only the first three have hypo-branchial segments (*h.br.*); these are larger than the hypo-hyal. The upper part of each arch is shorter than the lower; in the first four there is a single small ear-shaped pharyngo-branchial (*p.br.*); thus the last arch has only one piece on each side, and the last but one, three. The segmentation of the hyoid arch is thus seen to be very different from that of a typical branchial, which has no *interbranchial* piece, and the upper part of which is directly superimposed on the lower; moreover, I look upon the hyomandibular and symplectic as a divided *epi-hyal*, with no *pharyngo-hyal*, above.

D. *Transversely-vertical sections of the head of a young Sturgeon* 8 *inches in length.*

These sections show much clearer signs of the composition of the great ethmo-nasal tract than can be got from the outside views of dissected skulls; moreover, they display the curiously cancellated and burrowed condition of the very hard hyaline cartilage. There is generally some fatty tissue imbedding the vessels that run in these burrows and spaces.

Section 1.—The first of these (Plate 15, fig. 14) is through the end of the beak, and the "prenasal rostrum" or intertrabecula (*i.tr.*) is depressed or spindle-shaped in section; rough dermal bones are seen surrounding it.

Section 2.—In the next (Plate 15, fig. 15) the cornua trabeculæ (*c.tr.*) are cut through at their fore end; they are depressed at this part, sub-concave above, rounded below, and attached by a narrow isthmus to the top of the intertrabecula (*i.tr.*) which is sub-triangular here, and dilated and convex below. A rounded chink separates these three pre-cranial elements almost to their roots. The dermal bones form a flat upper, a round lower surface, and a lobate side.

Section 3.—Here (Plate 15, fig. 16) the three elements have become fused together, but the burrowing vessels and the fatty tissue show the original line of union of the parts. The form of the triple rostrum is, above, concave at the middle, and convex at the sides; below, concave laterally, and convex at the middle.

The dermal covering takes the same form, but the sides are notched; here, as in the last, a sub-marginal groove, right and left, appears, below.

Section 4.—Here (Plate 16, fig. 8) the enlarging beak shows a more rounded cartilaginous pith, but is very similar to the last; this is more than half way to the nasal capsule, behind.

Section 5.—In this (Plate 16, fig. 9) the rostrum, close in front of the nasal capsules, has become multiangular; the cornua trabeculæ (*c.tr.*) are again united merely by an isthmus to the intertrabecula mass; they are thick, almost bilobate, and descend obliquely; they are separated by a semicircular notch, laterally, from the middle part (*i.tr.*); below, also, a similar concavity is seen, right and left, but twice as large as those on the sides. Between the latter the intertrabecula is a rounded beam; above, it is concave, and on each side has a lateral angle which bounds the lateral notch. The bones outside carry out this ridged form; below, a thick squarish mass of bone is seen, which is one of the vomerine series (*v.*).

Section 6.—Here (Plate 16, fig. 10) the olfactory sacs (*ol.*) are cut through their middle, and here the angulation of the parts is intensified; the cornua trabeculæ (*c.tr.*) are now large wings, pedate at their free ends, and are separated laterally from the intertrabecular mass (*i.tr.*) by a very large semi-circular notch, in which the nasal capsule lies. Here the intertrabecula forms a roof over the sac, right and left, and it is very hollow above; below it is burrowed by a vomerine scute (*v.*), and is becoming

narrower, and more like a distinct beam; here also the outer bones do but fringe and enlarge the section.

Section 7.—In this (Plate 16, fig. 11) section the antorbital wall is exposed, behind the nasal sacs; that wall is composed of the aliethmoids (*al.e.*) and the ethmo-palatines (*e.pa.*). Here the paired cartilages are the trabeculæ (*tr.*) for this section is behind the cornua; but the intertrabecula (*i.tr.*) is very large from top to bottom. The middle region of the intertrabecula is the perpendicular ethmoid (*p.e.*), on each side of which the olfactory nerves (I.) are escaping; its alæ above are becoming the superorbital bands (*s.ob.*), whilst below, its huge beam is burrowed by a vomerine bone (*v.*).

Section 8.—In this section (Plate 16, fig. 12) the eye-ball (*e.*) is just caught, and the cranial cavity laid open at the olfactory foramina, with their nerves (I.); the rest is very similar to the last section; in both, dermal bones defend the sides of the face, and above, the frontal scute is cut through.

Section 9.—This (Plate 17, fig. 1) is through the middle of the orbit, where the superorbital band (*s.ob.*) narrows in; here the supercranial valley is very large and deep, and the section of the skull has the shape of an Ox's face. In this young specimen the chondrocranium is very massive, and the pyriform cavity for the hemispheres (C^{1a}.). is only one-fourth as large as the section itself, which is widest below, and rather pinched in the middle. The skull, below the cranial cavity, is as deep as the cavity, and is burrowed, below, by the splintery fore end of the huge parasphenoid (*pa.s.*); the swelling cartilage on each side belongs to the trabeculæ (*tr.*) the middle part to the intertrabecula (*i.tr.*). The orbital muscles (*or.m.*) are planted in chinks of the basal mass.

This section is in front of the mouth and through the front of the upper lip (*u.l.*); there is, here, a crescentic cavity, with the horns below.

Section 10.—In the next section (Plate 17, fig. 2) the small eye-ball is just missed, but the optic nerves (II.) are seen emerging from the brain (C^{1a}.). Here the cavity is something like an hour-glass, being as wide below as above; the tegmen cranii (*t.cr.*) is twice as thick as in the last, and the basal mass (*tr.*, *i.tr.*) only half as thick, for this is behind the lobes that envelop the parasphenoid (see Plate 16, figs. 1–4).

Here the superorbital bands are wider and more solid, and externally, a new plate of cartilage has come in, on each side from the eaves of the hind skull; this is the sphenotic (*post-frontal*) lamina (*sp.o.*). The solid basal plate is grooved sub-laterally and in the middle, and the parasphenoid (*pa.s.*) fitting to these sinuosities is, in section, like a stretched bow.

Below the base of the skull there is a quantity of very lax tissue, permitting the greatest freedom to the movements of the protrusible oral apparatus, and below this we see the large arched mass of the "adductor mandibulæ" muscle (*ad.m.*) on each side. Below the muscles, the fore part of the pterygo-quadrate cartilages (*pg.q.*) are cut through, and they are flanked by the maxillary and palatine bones (*mx.*, *pa.*) the former outside, and the latter beneath.

The mouth is nearly closed, the upper and lower lips, as in the next section (*u.l.*, *l.l.*), are seen with their rugæ, but without their teeth, and in the lower lip the mandibles (*mk.*) are just brought into view.

The parietal scutes were cut through above, and post- and sub-orbitals were seen, at the sides, and below, but not figured.

Section 11.—In this section (Plate 17, fig. 3) the sphenotic lamina (*sp.o.*) is thicker, but is still separated by a notch from the tegmen cranii (*t.cr.*); that part is thinner in the middle, and deeply concave. Here the cranial cavity has widened, for the section is close in front of the mid-brain. The section, now, is that of an Ox face with drooping horns, and the muzzle is now narrower around and under the infundibulum (*inf.*). On account of the very small size of the eye-ball (Plate 17, fig. 1, *e.*) *four* of these sections are between the eye and the ear; in this the orbital wall (*o.s.*), which is extremely thick, is twice scooped for the orbital muscles and the fatty masses that occupy the orbit—much too large for the eye-ball. Here the intertrabecula has died out, and the trabeculæ (*tr.*) have united directly with each other, and the plate thus formed has lost half the thickness seen in the last section (Plate 17, fig. 2, *tr.*, *i.tr.*).

The primary form of the trabeculæ is still seen at the sides, below, and the whole of the basal plate is crenate, making the parasphenoid (*pa.s.*) assume an undulated form as it follows the risings and fallings of the cartilage. In this section the oral apparatus is cut through the middle, and the opening itself is crescentic below, with a notched upper outline; this is due to the projection right and left of the pterygo-quadrates (*pg.q.*) and their investing bones, the palatines (*pa.*, *pg.*).

Here, the cartilages covered by the large adductor muscles (*ad.m.*) are sigmoid in section, and besides the outer bones, the pterygoids (*pg.*) now show themselves, both as an inner and an outer section, being through their forks. The quadrate region, with its orbitar process (*q.*, *or.p.*) is separate, now, and over it is the maxillary (*mx.*); to the quadrate the mandible (*mk.*) is articulated, it then passes almost directly inwards towards its fellow, which it does not quite meet; the dentary (*d.*) is seen flanking the Meckelian rod.

Section 12.—In this section (Plate 17, fig. 4) the cranial cavity is Y-shaped, and contains the front of the mid-brain above the fore-brain (C^1.), with the infundibulum passing into the pituitary body (*py.*). Here, in front of the post-clinoid wall, the alisphenoidal region (*al.s.*) is extremely thick—twice as thick as the tegmen (*t.cr.*) and the continuous sphenotic wings (*sp.o.*).

In this section the parts round the mouth are like those of the last, but the foremost azygous metapterygoid (*mt.pg'.*) comes into view, and the mandibles (*mk.*) are cut away, distally.

Section 13.—This (Plate 17, fig. 5) is through the middle of the mid-brain (C^2.), and the back of the pituitary body (*py.*). The post-clinoid wall, which is an oblique shelf running forwards and a little upwards (Plate 16, fig. 2, *p.cl.*), is here cut through obliquely so as to appear thicker than it is actually. This section seems to show

the pituitary body as lying in a separate and very solid box, for the rest of the skull is quite distinct from it, above. This arises from the fact that the foramina ovalia are here, with the trigeminal nerves (V.); the alisphenoidal wall, the roof, and the thickened sphenotics are seen in the upper part of the section. The parasphenoid (*pa.s.*) curls round the flatter base, the parietal (*pg.* by mistake for *p'.*) and post-orbtial scutes were cut through. Below, the adductor mandibulæ muscles (*ad.m.*), the pterygoid cartilages and bones (*pg.q.*, *pg. q.*, read *pg.*) are severed, and the latter are in one piece, for this is behind their great notch. The smaller azygous metapterygoid (*mt.pg'.*) is seen; the extreme angle of the quadrate (*q.c.*); and the hinge and part of the shaft of the mandible (*mk.*) through the dentary and the pre-opercular bones.

Section 14.—Here (Plate 16, fig. 6) the breach in the lower part of the walls is repaired, for this is behind the foramina ovalia, and through the fore part of the auditory capsules (*au.*); the ampulla and front part of the arch of the anterior canal (*a.s.c.*) are laid open. The roof is thicker and flatter; the sphenotic wings (*sp.o.*) are still large and thick; the cavity of the skull is single, narrower, and is half a long ellipse in shape, the angles of the broad upper end being rounded. Here the notochord is not seen, it has retreated too far backwards, but the parachordal mass (*iv.*) is hugely thick, and is wider; it is close behind the post-clinoid wall. The fore part of the hind-brain (C^3.) is cut across, where it is giving off the facial nerves (VII.), close behind the roots of the trigeminals (fig. 5, V.). The last section was cut through the interspace between the pterygoid band and the orbitar process (fig. 5, *pg.q.*, *q.c.*; and see also Plate 16, figs. 1 and 7); here the back of the suspensorium (*q.c.*) is cut through, at the hind part of the maxillary bone and the orbitar process (*mx.*, *or.p.*). A notch seen in the hind margin of the pterygo-quadrate cartilage (Plate 16, fig. 5, *pg.q.c.*) is cut across here, and the median part of the cartilage crops up, again, right and left; between these the main azygous metapterygoid (*mt.pg'.*) is seen. The angle of the mandible (*mk.*) and the end of the dentary (*d.*) are also cut across.

Section 15.—In this section (Plate 17, fig. 7) the chondrocranium attains its greatest solidity, and here the small cranial notochord (*nc.*) has its point cut through. The sphenotic has given place to the "pterotic" region, the arch of the anterior and the ampulla of the horizontal canals (*a.s.c.*, *h.s.c.*) are exposed, and so also is the auditory nerve (VIII.), as it arises in the hind-brain (C^3.) and runs through the meatus internus into the vestibule (*vb.*). Here the tegmen cranii is thick and concave, and the pterotic expansions (*pt.o.*) are very rough and lobulate. Under the bulging sinuous parachordal mass the parasphenoid (*pa.s.*) has become very wide, and now sends down its free edges. Under the capsules the "protractor hyomandibularis" muscles (*pt.hm.*) are seen as huge triangular masses, and the "adductor mandibulæ" muscles (*ad.m.*) are cut through in their hinder part. A little of the pterygoid region (*pg.q.*) and the hind angle of the quadrate (*q.c.*) come into view, and between the former the median and main lateral metapterygoids (*mt.pg'.*, *mt.pg''.*). The deepest part of the pterygoid bone (*pg.*) is seen flanking the inner face of the suspensorium. Under the quadrate

a new and thick cartilage appears; this is the symplectic (*sy.*), it is crescentic in this, its front edge (lower end), and between it and the quadrate there is a small nucleus of cartilage which will be described in the next stage—it is a "suspensorial ray" (*sp.r.*). The chief scutes seen are the parietals; the squamosal, the opercular, and the sub-opercular, also, may be traced at this point, but are not figured.

Section 16.—In this slice (Plate 17, fig. 8) we see several new parts come into view below; above, the skull is altogether flatter, and the supercranial valley narrower. The auditory nerve (VIII.) is still shown, also the arch of the anterior and horizontal canals (see also fig. 7, *a.s.c.*, *h.s.c*). The basal plate (*iv.*, *nc.*) is very irregular, as it passes into the auditory capsules, right and left; the parasphenoid (*pa.s.*) partakes of this irregularity, and here its decurved wings are larger. The compound meta-pterygoid plate is composed at this hind part of a large middle, two large lateral, and two lesser intervening plates (*mt.pg′.*, *mt.pg″.*). The top of the hyomandibular is just seen and most of its great protractor muscle (*pr.hm.*); below, the symplectic is cut through from top to bottom. Below the wide oral cavity the cerato-hyal (*c.hy.*) with a thin ectosteal coating, the hypo-hyals (*h.hy.*), the fore part of the basi-branchial (*b.br.*), and the fore end of the first hypo-branchials ($h.br^1$.) are also seen. The scutes are very similar to those of the last.

Section 17.—In this (Plate 17, fig. 9), the cranial valley is seen to be wider again; the auditory sacs are cut through where the posterior canal (*p.s.c.*) is descending, and the whole structure is lessened laterally; a thin pterotic eave (*sp.o.*, read *pt.o.*) grows down on each side. Here the hind-brain (C^3.) is less, and it is giving off the roots of the large vagus nerve (X.) whose ganglion root and stem are laid bare. Here we still see that the auditory sacs are open to the skull (or only closed by membrane), and here the sacculus (*s.*) is seen hanging from the rest of the vestibule (*vb.*). The notochord (*nc.*) is becoming larger, and the thick curved basal plate (*iv.*) is here separate from the auditory capsules; below it the parasphenoid (*pa.s.*) is thick, and at its notched sides we see a pharyngo-branchial (*p.br.*) and outside this part of the gills (*g.*). The lower part of the hyomandibular, part of the symplectic, inter-hyal, and cerato-hyal (*hm.*, *sy.*, *i.hy.*, *c.hy.*) are cut across; and near the mid line the basi-branchial, the first cerato- and hypo-branchials, and the second hypo-branchials (*b.br.*, $c.br^1$., $h.br^1$., $h.br^2$.).

Section 18.—In this section (Plate 17, fig. 10) the post-auditory fontanelle is just missed, and we see that it must answer to the interspace between the supra-occipital and first vertebral arch; for the chondrocranium (see Plate 15, fig. 13) sends its copious growths over the proper spinal region. The cavity here is very large, this being, indeed, the "foramen magnum," and the ex-occipital walls are very thick, and almost vertical. The hinder part of the vagus nerve (X.) is still seen in the chink which separates—up to this point the sides form the base, which is increasingly massive, but has not a very large notochordal section (*nc.*) in it. The parasphenoid (*pa.s.*) is beginning to break up at the middle; outside it a pharnygo-branchial is

seen (*p.br.*), and outside that the most backwardly projecting part of the massive hyomandibular (*hm.*).

Section 19.—The last of this series (Plate 17, fig. 11) is post-cranial; the ganglion of a spinal nerve (*sp.n.*) is cut across; the medulla spinalis (*my.*) is seen to be very small in proportion to the spinal cavity, and the notochord (*nc.*) is twice as large as in the skull, and reaches the theca vertebralis. The parasphenoid (*pa.s.*) is in two parts (see Plate 16, fig. 3); the hind and transverse processes of the undivided vertebral tract are very large, and are covered with large scutes. This section is behind the operculum (Plate 15, fig. 10, *op.*), and through one of the hinder branchial arches; in the general branchial recess, the pharyngo-, epi-, and part of the cerato-branchials (*p.br.*, *c.br.*, *e.br.*) of a middle gill arch, and some of the gills, are shown.

Behind this part the notochord becomes thicker, and its chondrified sheath more distinct; the forked parasphenoid dies out, and the *neuro-central* cartilages appear (Plate 16, fig. 3).

Fifth Stage.—Adult Sturgeon (Acipenser sturio).*

The Sturgeons dissected for this stage were about 4 or 5 feet long, such as are most commonly seen in the markets; my last stage is from a much larger specimen, but not from the largest. Dr. GÜNTHER ('The Study of Fishes,' p. 362) says that this species attains a length of 18 feet.

The swelling of the fore part of the trabeculæ and intertrabecula in the orbital region becomes very remarkable, and the cartilage becomes subdivided into an upper and a lower stratum; between these the parasphenoid (Plate 18, fig. 3, *tr.*, *i.tr.*, *pa.s.*) grows as a thin dentate lamina, with one very long median spike. The clavate swellings of the trabeculæ bind on the sides of the exposed part of the parasphenoid, and the *second floor* of cartilage in the middle (*i.tr.*) runs up to the base of the huge rostrum, appearing below as a rounded elevation, separated from the lateral lobes by a deep sulcus, which is filled with fatty tissue. In the fatty tissue outside the paired lobes of cartilage there is a series of four thin cartilaginous plates (*e.pa′.*); they are outside the trabeculæ, and behind the ethmo-palatine boundary of the nasal sac, and probably represent, partly, as Mr. HOWES suggests, the free ethmo-palatines of other kinds; in Siredon I have shown that there are two of those cartilages on each side (Phil. Trans., 1877, Plate 24, figs. 1–3, *e.pa.*, *pt.pa.*)—an "ethmo-palatine" and a "post-palatine."†

* The dissections, figures, and notes for this stage were made for me by my friend Mr. GEORGE HOWES, Professor HUXLEY'S talented Demonstrator.

† I wish to put all these *pre-oral* growths together for comparison, in hope of obtaining a clue to their real nature. Mr. BALFOUR'S writings have made me very doubtful of the view that, at one time, seemed to me to be almost demonstrable—viz., that these antorbital cartilages were in reality the rudimentary upper part of a *pre-mandibular visceral arch*, but their position, in front of the hypoblast, makes their determination as difficult as that of the *pro-chordal* part of the basis cranii.

The most important further modifications to be seen in these large individuals, are in the visceral arches.

There are seven arches, and the whole series is displayed in a side view (Plate 18, fig. 5) so as to show their relative size, and their varied modification; in that figure the inferior part of the hyoid arch is shown as drawn backwards towards the first basi-branchial (*c.hy.*, *b.hy.*, *b.br*[1].); in reality it runs across to meet its fellow in the floor of the mouth (fig. 10, *c.hy.*, *b.hy.*).

The two first arches, the mandibular and hyoid, are intensely specialised; the other five are very similar to those of the Elasmobranchs, save that they have some of the larger bars partly ossified; and are still more like the branchial arches of Holostean Ganoids and Teleosteans. The upper elements of the mandibular arch, the right and left "suspensoria," are transformed into the oblique convex roof of the very mobile protrusible mouth, and the free mandibles are made to be antagonistic to the antero-inferior part of this complex structure. Each cartilaginous suspensorium is a broadly falcate plate, whose arched upper border comes in contact with that of its fellow in front and above; below and behind, it suddenly bends forwards and becomes very solid, to form the quadrate condyle (figs. 4, 5, *q.c.*). The whole plate is gently and sinuously convex above and concave below; behind, over the hinge, it thickens into a rib-like enlargement, and grows outwards and forwards as a superficial "orbitar process" (*or.p.*). The upper margin is arched regularly until near the hinge, and then is hollowed a little; the lower margin is twice-notched and concave. The bones applied to these pterygo-quadrate plates have not caused the absorption of the cartilage in this stage, which is *relatively* more extensive than in the last stage, in which the hind margin was notched. The outermost bones are the largest; they are the maxillaries (*mx.*), they are strongly bowed, dilated most where they meet in front of the cartilaginous plates, and to a lesser degree where they bind upon the orbitar processes behind. A large space for each "adductor mandibulæ" muscle exists between the maxillaries and the pterygo-quadrate cartilages. Another superficial bone stands upright on the hind end of the maxillary; it is a high triangle, and its base is below. It binds on the thick, ribbed, outer edge of the suspensorium in its quadrate region; this is the small "pre-opercular" (*p.op.*), whose almost equally small counterpart exists in *Lepidosteus*. Along the lower edge of the cartilage, in front, a very jagged little bony scale is seen, overlapped by the fore end of the maxillary. This is the mesopterygoid (*ms.pg.*); it was not a separate bone in the last stage. Behind it there is a small style, with its sharp end behind, reaching to the end of the foremost and larger notch; this is the palatine (*pa.*). Inside the plate (*pg.q.*) there is a large parostosis, the pterygoid; it lines all the cartilage except a falcate tract in front and above; this causes it to be sharply notched in front; this form is well shown by the shading of the cartilage (Plate 18, fig. 4).

The mandible or Meckelian rod (Plate 18, figs. 5 and 8, *mk.*) is a very short stout cartilage like that of a Tadpole; the condyle is convexo-concave, and the angular

process is large and projecting. That is the only part not covered, on the outside, by the flattish but thick dentary bone (*d.*). On the inside (Plate 18, fig. 8, *d.*) it shows a large crescent of bone, where the rod becomes slenderer in the middle. Behind that part, on an apophysis of the cartilage, a small oblong second bone appears. This is the coronoid (*cr.*); its direction is backwards and a little downwards. The distal end of the rod is thick and massive, and is united to its fellow by ligamentous fibres.

A small squarish suspensorial ray is seen behind the angle of the mandible (Plate 18, fig. 5, *sp.r.*); it is far below the usual place for the spiracular cartilage of a Shark. The other half of the general roof of the mouth is fan-shaped (Plate 18, figs. 4 and 5, *mt.pg'.*, *mt.pg''.*), the narrow handle running in between the two pterygo-quadrates, and the outspread part growing round their convex hind margin. Thus this complex plate has two convex edges behind and two concave edges in front; then it runs to a sharp point between the symmetrical plates. The earliest pieces of this patchwork are still the largest; they are the main azygous plate and the main symmetrical plates (*mt.pg'.*, *mt.pg''.*); the single piece is like the bowl of a spoon, but longer; the other two are roughly three-cornered. Outside, between the latter and the quadrate region of the paired plate (*q.c.*) there is a much smaller but tolerably constant piece on each side. Behind, between the three main patches, there are three or four on each side, inconstant in number and form; and in front, in the interspace between the three main patches and the pterygo-quadrates, there is a patch or two on each side, and then a single row of four or five, lessening forwards. These patches are all set in one common web of fibrous tissue, so as to look, in a rough dissection, like one unpaired hard-palate plate.

Half this complex palate of pterygo-quadrates and metapterygoids is nearly equal in length and width, but far inferior in thickness, to a single hyomandibular (Plate 18, fig. 5, *hm.*). That segment has no "serial homologue" either before or behind it, for the subdivision of the upper part of the visceral arches is different in the mandibular, hyoid, and branchial arches. The hyomandibular is not the *uppermost* segment of a normal visceral (*branchial*) arch, for there is no pharyngo-hyal in this type. Nor does it correspond to more than the upper two-thirds of an epi-branchial; the lower third is the separate symplectic (*sy.*). Neither does it harmonise with the pier of the arch in front, which is segmented quite after another fashion; there, the part answering to the symplectic is the pterygoid foregrowth of the suspensorium, whilst the part which should correspond to the head of the hyomandibular is partly continuous with the head of the pier of the opposite side, and largely broken up into a tesselated pavement of irregular segments. The *upper* "epi-hyal" (*hm.*) is, above, a normal phalangiform segment, but below and behind it expands into a huge pedate plate; the "toe" below, is tied to the next segment, the "heel" behind, carrying the "opercular," and answering to the opercular process in Teleostei; this convex pedate slab is almost entirely unossified.

The neck and shoulders of the hyomandibular are ossified, so as to leave the round convex head and expanded lower part unchanged. The osseous shaft is hour-glass-shaped, very thick, and leaving only a small core of cartilage unossified (Plate 18, figs. 5–7, *hm.*); this bony tract is very angular, in section, and somewhat four-cornered. On the outside of the bony sheath, embedded in the periosteum, there are simple and forked cartilages (Plate 18, figs. 5, 6, 7, *hm.r.*), evidently rudimentary "branchial-rays;" as seen in the sections (figs. 6, 7) they are very solid, "and usually exist upon (*a*) the anterior, and (*b*) the outer face only; in one specimen, however, (fig. 7) they also occurred upon the anterior and inner" (Howes); they are very variable as these sections show.

The "toe" of the hyomandibular (*hm.*) rests upon the upper face of the upper end of the next segment, the symplectic or lower epi-hyal (Plate 18, fig. 5, *sy.*); the two are attached together by a strong fibrous joint. This distal segment of the hyoid "pier" is half the length and half the medium width of the upper piece; it is phalangiform, straight, and thick. Distally it is attached by a strong fibrous joint to the quadrate region (*q.c.*), which it carries; proximally, at its proper upper end it is articulated to the inter-hyal (*i.hy.*); it is wholly unossified.

The intercalary segment, or "inter-hyal" (*i.hy.*) is a sub-cubical, lobulated mass of cartilage, interposed between the symplectic and the lower element of the hyoid arch, the cerato-hyal (*c.hy.*). This latter segment in the undisturbed condition of the parts runs across and a little forwards under the throat; it is about the size of the symplectic, but more slender and has a narrow waisted ectosteal tract a little below its middle. This bone is nearly half the height of the bar, is pinched and angular, has an unossified pith and extra-hyal cartilages (Plate 18, fig. 9, *c.hy.*, *c.hy.r.*), like the hyomandibular.

There is a thick wedge of cartilage segmented off from the cerato-hyal, the hypo-hyal (*h.hy.*); it is attached by fibrous tissue to its fellow, the related ends being narrow, and also to the fore end of the first basi-branchial (Plate 18, figs. 5 and 10, *h.hy.*, $b.br^1$.).

The thick, solid, strongly bent branchial arches (Plate 18, figs. 5 and 10) lessen and become simpler from before backwards. The joint between the main upper and lower segments (*e.br.*, *c.br.*) is a well formed "elbow," the upper part is a little less than the lower. Only the first and second branchial arches are perfect, and they have acquired an additional pharyngo-branchial (fig. 5), and these small segments rest on short forks of the epi-branchial (*e.br.*). There is only one pharygno-branchial on the third arch ($p.br^3$.), and that on the fourth has (evidently) become fused with the epi-branchial ($e.br^4$.). The fifth arch is in one piece, it is a cerato-branchial (fig. 10, $c.br^5$.), and like the four cerato-branchials in front of it, has a bony tract in its middle part. Only the first and second epi-branchials ($e.br^1$., $e.br^2$.) have ectosteal tracts. On the first of these there are at least two imperfect "rays" (*br.r.*), as on the arches in front. The lower part of each arch is bowed outwards, the upper is sigmoid, and they are very

angular, especially where the ectosteal tract exists. Only the first three have hypobranchials (Plate 18, figs. 5 and 10, $h.br^{1-3}$.); these begin much larger than the hypohyal and then lessen backwards; they are flat, finger-shaped, and not ossified.

Another addition of cartilaginous segments has taken place below; in the young Sturgeons (Plate 14, fig. 5, and Plate 16, fig. 5) there was only one basi-branchial carrying the three first arches. Now, *three* new smaller segments have appeared ($b.br^{4-6}$.), the last of these is wedge-shaped, and belongs to a suppressed arch, for it passes behind the pedate end of the arrested fifth arch; the foremost piece belongs to three arches.

These piers are compressed, and the first, which belongs to *three* arches ($b.br^{1-3}$.), is nodose.

Sixth Stage.—Skull of an unusually large Sturgeon* (Acipenser sturio) (*in the Hunterian Museum*).

This very valuable specimen of a much older individual, shows some very important modifications, which have, as it were, *an upward look* towards the Holostean Ganoids and the Teleostei.

In the last stage the pterygo-quadrate cartilages were even more perfect than in the young of 7 or 8 inches in length. In this specimen, however, the "parostoses" have caused a considerable amount of absorption of the hyaline cartilage, just as the dentary, normally, causes MECKEL's cartilage to shrink and even become absorbed; but I cannot find any evidence of a direct *ectosteal* relation of the bone to the cartilage. The pterygoid bone (Plate 17, figs. 12, 13, *pg.*) gets over to the *outer* side over the convex inner margin, and causes the absorption of the cartilage in that region. Moreover, the jagged bony tract which represents the mesopterygoid, and which in the last was at the antero-inferior edge of the cartilage, is now (Plate 17, figs. 12 and 13, *ms.pg.*) a sharp wedge of bone filling up the space between the forks of the pterygoid on the inner side (fig. 13), and is seen as an oval plate of bone nearer the top than the bottom, on the outer side (fig. 12, *ms.pg.*). These differences are not all due to *age;* there is a considerable amount of variation in individuals of the same age in these types, where the sub-cutaneous and sub-mucous bony tracts are but *deeper scutes,* and where the chondro-skeletal regions are so generalised and, as it were, *hypertrophied.*

With regard to the *buried scutes,* we see a right and left variation in this same specimen (Plate 18, figs. 1 and 2, the *right* and *left* orbital region in this large skull).

Here there are no proper *ectosteal* prefrontals (ecto-ethmoids), orbito-sphenoids, alisphenoids, or prootics; but, since the last stage, parosteal tracts have appeared in all those places; they are *deep* "scutes," not *shallow* endo-skeletal elements, and are the prophecy, so to speak, of the special "ectostoses" seen in the Holostean Ganoids and the Teleostei, and in all the types above them. Round the thick antorbital

* Even this specimen was not half the size this species sometimes attains to.

(ecto-ethmoidal) mass of cartilage I find a thin but rough irregular layer of bone, just where the Teleostei have their proper ecto-ethmoid (Plate 18, figs. 1 and 2, *e.eth'.*). Also over the optic foramen (II.) there is a very large splint (*os'.*) applied to the orbital cartilage; it runs upwards and forwards. On the *right side only* (fig. 1, *al.s'.*) there is a much smaller plate in the alisphenoidal region, and *behind* and partly *round* the foramen ovale (V.) a thin semi-annular plate (*pro'.*) representing the prootic of the higher types. But no direct grafting of bone on the cartilage can be seen, and the *affinity* of the bone for the cartilage or, *vice versâ*, of the cartilage for the bone, is here extremely feeble; there is no material interaction; the co-ordinating force, however, has produced a plate of the proper form, and put it ready for use in the proper place.

Summary and comparison with other types.

It is evident that we have in the Sturgeon a form which is practically intermediate between the Selachians and the Osseous Ganoids (Holostei); the form of the larvæ (Plate 12) suggests this view at once. I must again refer the reader to the researches of SALENSKY and BALFOUR on the embryology of this type; my own recapitulation and comparison must be confined to the cephalic skeleton.

A. *The primordial skull.*

We saw that in the larvæ of *Acipenser ruthenus* only about a third of an inch in length ($9\frac{1}{2}$ millims.) the "embryonic cartilage" had largely become "hyaline;" that the foundations of the cranium were laid, and the visceral arches were differentiated and becoming quite solid. Here, it would seem, that in so small a larva of so large a Fish—and that Fish lying at the base of the great *archaic* group of the Ganoids—we have a good chance of seeing the primordial vertebrate skull in its utmost simplicity. The fact is, that we have *a confusingly simple* state of things.

In the fore part of the spine, as well as in the whole basi-cranial region, the paired skeletal tracts that lie right and left of the *mesoblastic sheath* of the notochord, the hardening cartilage shows no signs of segmentation or *intercalary vertebral subdivision;* this is just like what occurs in the Selachians (Trans. Zool. Soc., vol. x., plate 35). Moreover, this Chondrosteous Ganoid remains in this condition, as far as I can find, throughout life, and does not acquire the occipito-cervical articulation, so well known in the Selachians, but which in them is a secondary modification of the parts. By careful comparison of all the facts I have been able to gather by observation of many types and at many stages, I cannot help coming to the conclusion that the *normal intercalary vertebral segmentation* with which we are so familiar in the post-cephalic region of the Vertebrata, generally, is *a comparatively late and secondary specialization* in the evolution of this, the highest, group of animals.

If Mr. BALFOUR's suggestion ('Comp. Embryol.,' vol. ii., p. 366) be true, viz.: that the fore-brain with its special optic and olfactory outgrowths is a sort of outgrowth or

addition, itself, to the neural axis, then we have to reconsider the meaning of any and every part of the cranial skeleton which may be formed in front of the notochord and of the overlying and overfolded mid-brain.

Thus all the *prochordal* cranial, and all the *pre-mandibular* facial growths of the skeletal cartilage have to be subjected, again, to the severest morphological inquisition under that light—the light of Embryology—which alone can make manifest their true meaning.

If the notochord be the true organic axis of the skeleton of the animal, and if the visceral (or branchial) arches were only developed in relation to the hypoblastic branchial outgrowths of the dilated respiratory pharynx, then it seems to be necessary that we should consider all the skeletal parts in front of those structures as superadded specializations of, or "outgrowths" from, the front end of the proper Vertebrate form.*

In certain types, namely, the Lamprey, the Selachians, the Urodela, and the Anura, the trabeculæ are chondrified before the hinder or parachordal tracts. Nevertheless, the posterior part of the trabeculæ in them is parachordal; the rest, up to the "atlantal" region, may afterwards chondrify separately, as in the Urodela, or continuously, as in the others.

In *Acipenser*, *Lepidosteus*, and *Salmo* I find no difference of time in this matter, and should therefore be inclined to look upon the earlier growth of the trabeculæ as due to the special weight and pressure of the fore-brain in those cases, and as a non-essential modification, just as I consider the later segmentation of the trabeculæ from the investing mass in *Salmo* and *Chelone*, and to a less extent in Crocodiles and Birds, as a non-essential specialization.

Yet the trabeculæ are as truly part of the proper mesoblastic axial skeleton as the fore-brain is part of the proper epiblastic neural axis.

The whole of the *pre-cerebral* tracts of the skull, namely, the cornua trabeculæ and the greater part of the intertrabecula—all of it that lies in front of the exit of the olfactory nerves—I should consider to be mere *outgrowths* or "apophyses" of the cranial skeleton.

The axial skeleton is more aborted in front than the axial nervous system, even if the fore-brain is reckoned as an additional part, for the mid-brain bends completely over upon itself, and the notochord only partially. Yet, as I have shown in *Chelone viridis*, its cartilaginous mesoblastic sheath is continued downwards as solid cartilage below and in front of the end of the notochord. I am inclined to think that the intertrabecula is a breaking out again of that mesoblastic tract (a sort of cranial "spadix") but with its continuity, for a short space, interrupted.

The ventral part of the primordial skull presents as many difficulties as the dorsal; the post-oral visceral (or branchial) arches, which may be both *superficial and deep*,

* For my own part, I am quite content that this should be so, albeit my own descriptive language will have to undergo a considerable amount of evolutional modification, and many things that seemed to me, once, to be clear and certain, made dark and uncertain.

have to be compared with such facial growths as may exist in front of the mouth, and these, if possible, have their relation to the post-cephalic arches determined.

Long ago, to those who knew nothing of Embryology, all this seemed to be easy enough; now, with all the new, increased light from that source, the problem has become extremely difficult, and is certainly not solved, as yet.

I do not see that the superficial cartilages that surround the mouth have any right to be compared, serially, to the arches of the pharynx or of the chest; they appear to me to be the most *archaic* structures in the skeleton—"barbels," "labial cartilages," "nasal valves"—all these appear to me to be lineally descended from the inner supporting tracts of tissue of oral palpi, such as are met with in so many of the aquatic *Invertebrata*. The investing bones of the face may be grafted on such cartilages, but the two things are quite different in their nature. The condition of the visceral arches in this type, both in the larva and in the adult, has led me to reconsider the whole question of the nature of these arches.

There are several things to be considered at the outset, before a comparison is made of the skeleton of the throat, the branchial skeleton, and the skeleton of the chest. The post-auditory part of the cranium has manifestly undergone *secular* shortening, so that the pharyngeal or ventral region belonging to it often extends under the *twice-segmented* spine, whose fore part is, so to speak, intercalary or superadded, and does not correspond with the arches beneath it, which often extend backwards for some distance.

At one time this appeared to me to be an explanation of the fact that the inner (or proper) branchial arches of Fishes are developed beneath the fore part of the spine and the hind part of the basis cranii, whilst the mandibular and hyoid arches, the first and second of the branchial category, often fix themselves to the basal plates of the cranium.

I now strongly suspect this view of the matter to have been a mistaken one; and that it is the *abnormal size* and *special modification* of the mandibular and hyoid arches that make it necessary for those arches to seize hold of swinging points above their normal dorsal region or apex.

I think that the figures I have given of the visceral arches in the larval Sterlet (Plate 13, figs. 6 and 11) will make my meaning plain. Here only one arch is attached to the edge of so much of the parachordal plate as may creep under the auditory capsule; all the other arches are fairly under the head and forepart of the neck.

This normally inferior position of the visceral arches is best seen however in the early embryo of the Skate (see in "Pristiurus," Trans. Zool. Soc., vol. x., plate 35, fig. 4), where the metapterygoid, hyomandibular, and all the pharyngo-branchials, are shown *in situ*, after the whole cranium had been removed from above.

The sub-division of the pleuro-peritoneal cavity by the hypoblastic branchial pouches in the early embryo, the rapid closure of those cavities (the "head-cavities"), and the relation of the skeletal bars of the pharynx and mouth, whether deep or superficial—all

these things have to be carefully reflected upon before any classification of these ventral arches can be made.

It seems to me that a cartilaginous arch developed *inside* a recently-closed "head-cavity" must be a part of the "splanchno-pleure," and that a cartilage developed outside such a recently-closed cavity must belong to the "somato-pleure." *

The *ribs* belong to the outer lamina of the body-wall of the embryo, so also, it appears to me, do the "extra-branchials" of the Lamprey, the Tadpole, and the Shark.

If all this be true, the normal "intra-branchial" arches have no counterparts whatever in the skeleton of the trunk; they culminate in the class of Fishes, and are imperfectly developed, not only in the Abranchiata, but also in the degenerate Marsipobranchii, and the metabolic Amphibia Anura.

The extra-branchials of some of these latter types, and of the Sharks, have some right and title to be classified as a sort of cephalic ribs, but perhaps that claim had better not be pressed for the present; it is safer for the Morphologist to keep certain things in solution, when any doubt remains, than to crystallize them into what may turn out to be obstructive error.

In the metamorphosis of the larval Sturgeon the additional parts are easily explained, and are, for the most part, due to mere increase of certain tracts of tissue, and super-additions of secondary nuclei of cartilage, and of various centres of ossification.

Moreover, the fact that the dermal scutes are largely dominated by the cartilaginous endoskeletal structures of the cranium and pharynx, however interesting from one point of view, is not of any great fundamental importance.

With regard to the great "shoots" of cartilage that grow out, forwards, from the primary basis-cranii, these are parts that undergo a most extraordinary amount of modification in various types; they are specialised superadditions to the essential skull, of great importance in *Taxonomy*, but of little account in that which is fundamental in *Morphology*.

Comparison with Polyodon.

The skull of the other principal existing Chondrosteous Ganoid type comes singularly near to that of the Acipenserine skull, and in some things is curiously unlike it. Near as *Polyodon* approaches in the structure of its skull to *Acipenser*, it differs in having no complex metapterygoid plate, in the feebler ossification of its visceral arches, and in the presence of three pairs of "endosteal" centres not to be found in the Sturgeon. The anterior palatine ectostosis placed just where both the mesopterygoid and palatine plates meet in the Sturgeon, is probably the true homologue of the palatine bones of the Holostean Ganoids; the presence of a small prootic and opisthotic brings us nearer in this case to those higher types. The much larger and more perfect "orbitar

* The branchial artery lies *inside* the head cavity, and afterwards, when the branchial arch is developed, runs up a groove on the *outside* of it (see BALFOUR's 'Elasmobranchs,' plate 14, fig. 13, *a*, p. 208; and 'Comp. Embryol.,' vol. ii., p. 472, fig. 328).

process" shows in Polyodon a nearer relationship to the larval Frog; the absence of a metapterygoid plate brings it nearer to the Sharks, and the three pairs of *ectosteal* centres to the Holostean Ganoids. (See BRIDGE, Phil. Trans., 1878, Plates 55–57.)

Comparsion with the Selachians.

The development of the basis-cranii and cranial walls in *Acipenser* is very similar to what is seen in the Selachians; and the after modifications are essentially alike, except that in the Sturgeon the cartilage is very massive, and the occipito-cervical articulation is not formed. The separation of a large symplectic, and a lesser inter-hyal segment, the complex metapterygoid plate, and the partial ossification of the visceral arches, are all modifications that separate this from the Selachian types.

Comparison with the Holostean Ganoids.

Most of the peculiarities which distinguish the skull in that group from that of a Sturgeon are so many steps in the direction of the Teleostean skull. To say nothing of the lighter build of the chondrocranium, the numerous ectosteal patches in the skull wall, the intenser ossification of the visceral arches, and the absence of a distinct symplectic cartilage (it may exist as a separate bony centre, as in the Teleosteans), all these things show how far the Holostei have become specialized beyond the chondrosteous *Acipenser*. An important modification occurs early in *Lepidosteus*, namely, that the palato-quadrate is continuous, at first, with the trabecula; the intertrabecula also appears earlier. I shall compare the skull of the Ganoids, generally, with that of the Teleostei, in my next paper, which will treat of the skull of *Lepidosteus*.

Explanation of the Plates.

Plate.	Fig.	Stage.		Number of times magnified.
12	1	1	Larva (recently hatched) of *Acipenser ruthenus*, $5\frac{1}{2}$ millims. long	17
,,	2	1	Larva of same, $6\frac{1}{2}$ millims. long	15
,,	3	1	Under view of head of same specimen	15
,,	4	2	Head of larva of same, $8\frac{1}{2}$ millims. long.; side view	15
,,	5	2	The same head; lower view	15
,,	6	2	The same head; upper view	15
,,	7	2	A larger larva of same, $9\frac{1}{2}$ millims. long	10
,,	8	2	Head of same larva; upper view	10
,,	9	3	A still larger larva of same, $13\frac{1}{2}$ millims. long . .	15
,,	10	2	First of a series of transversely vertical sections of a larva of *Acipenser ruthenus*, $9\frac{1}{2}$ millims. long .	40
,,	11	2	Second section of same	40
,,	12	2	Third section of same	40
13	1	2	Fourth section of same	40
,,	2	2	Fifth section of same	40
,,	3	2	Sixth section of same	40
,,	4	2	Seventh section of same	40
,,	5	2	Eighth section of same	40
,,	6	2	Side view of dissected head of another larva, $9\frac{1}{2}$ millims. long	$26\frac{2}{3}$
,,	7	2	Under view of head of larva of *Acipenser ruthenus*, $9\frac{1}{2}$ millims. long	14
,,	8	3	Head of a larger larva of same, $13\frac{1}{2}$ millims. long; under view	14
,,	9	3	The same object; upper view	14
,,	10	3	Horizontal section of head of a larva of the same, $13\frac{1}{2}$ millims. long	40
,,	11	3	Larva of *Acipenser ruthenus*, $13\frac{1}{2}$ millims. long; side view of dissected head	20
,,	12	3	Visceral arches of the same head; upper view . .	20

Plate.	Fig.	Stage.		Number of times magnified.
14	1	2	Larva of *Acipenser ruthenus*, $9\frac{1}{2}$ millims. long; vertical section of head	26
,,	2	3	Second horizontal section of larva of same, $13\frac{1}{2}$ millims. long (see Plate 13, fig. 10).	40
,,	3	3	Third section of same head	40
,,	4	3	Same head; basis cranii, upper view	20
,,	5	3	Same dissection as last; lower view	20
,,	6	3	Maxillary and dentary of same dissection; side view	53
,,	7	3	First of a series of sections of the largest larva of *Acipenser ruthenus*, $14\frac{1}{2}$ millims. long	30
,,	8	3	Second section of same	30
,,	9	3	Third section of same	30
,,	10	3	Fourth section of same	30
,,	11	3	Fifth section of same	30
,,	12	3	Sixth section of same	30
,,	13	3	Seventh section of same	30
,,	14	3	Eighth section of same	30
15	1	3	(Same sections as on last Plate, continued.) Ninth section of same	30
,,	2	3	Tenth section of same	30
,,	3	3	Eleventh section of same	30
,,	4	3	Twelfth section of same	30
,,	5	3	Thirteenth section of same	30
,,	6	3	Fourteenth section of same	30
,,	7	3	Fifteenth section of same	30
,,	8	3	Sixteenth section of same	30
,,	9	3	Seventeenth section of same	30
,,	10	4	Head of a young specimen of *Acipenser sturio*, 8 inches long; side view	$1\frac{1}{3}$
,,	11	4	The same; upper view.	$1\frac{1}{3}$
,,	12	4	The same; lower view.	$1\frac{1}{3}$

Plate.	Fig.	Stage.		Number of times magnified.
15	13	4	Dissection of head of same; upper view	$2\frac{2}{3}$
,,	14	4	First of a series of sections of same	8
,,	15	4	Second section of same	8
,,	16	4	Third section of same	8
16	1	4	Dissection of head of a younger specimen of same, $7\frac{1}{4}$ inches long; side view	$2\frac{2}{3}$
,,	2	4	A vertical section of the head of another specimen, 8 inches long	$2\frac{2}{3}$
,,	3	4	Dissected skull of young *Acipenser sturio*, 8 inches long; lower view	$2\frac{2}{3}$
,,	4	4	The same; and same view, with visceral arches attached	$2\frac{2}{3}$
,,	5	4	Visceral arches of same; upper view	$2\frac{2}{3}$
,,	6	4	Fore part of same object; lower view	$2\frac{2}{3}$
,,	7	4	Part of same as last; inner view	8
,,	8	4	Fourth section of same (see Plate 15, figs. 14–16) .	4
,,	9	4	Fifth section of same	4
,,	10	4	Sixth section of same	4
,,	11	4	Seventh section of same	4
,,	12	4	Eighth section of same	4
17	1	4	(Continuation of sections of head of *Acipenser sturio*, 8 inches long.) Ninth section of same .	4
,,	2	4	Tenth section of same	4
,,	3	4	Eleventh section of same	4
,,	4	4	Twelfth section of same	4
,,	5	4	Thirteenth section of same	4
,,	6	4	Fourteenth section of same	4
,,	7	4	Fifteenth section of same	4
,,	8	4	Sixteenth section of same	4
,,	9	4	Seventeenth section of same	4
,,	10	4	Eighteenth section of same	4
,,	11	4	Nineteenth section of same	4

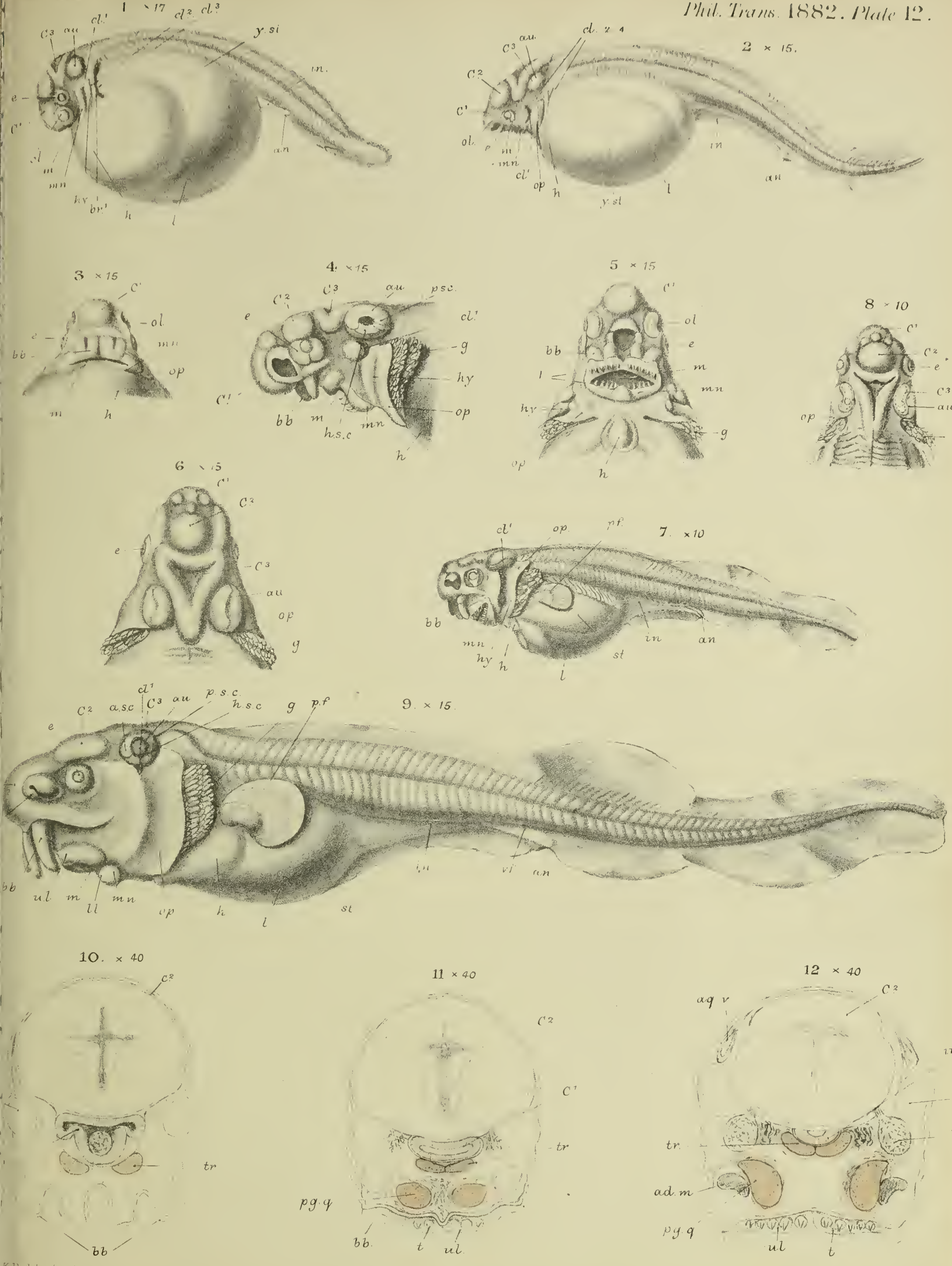
Plate.	Fig.	Stage.		Number of times magnified.
17	12	6	Pterygo-quadrate plate of old individual of *Acipenser sturio;* outer view . . .	$\frac{1}{3}$ natural size.
,,	13	6	The same; inner view	$\frac{1}{3}$ natural size.
18	1	6	Right orbital region of old specimen . .	$\frac{1}{2}$ natural size.
,,	2	6	Left orbital region of old specimen . .	$\frac{1}{2}$ natural size.
,,	3	5	Basis cranii, orbital region, in adult *Acipenser sturio*	Slightly enlarged.
,,	4	5	Palato-quadrate apparatus of same, from above	Slightly enlarged.
,,	5	5	Visceral arches of same, side view . . .	$\frac{3}{4}$ natural size.
,,	6	5	The same; section of hyomandibular . .	Slightly enlarged.
,,	7	5	The same; section in another specimen .	Slightly enlarged.
,,	8	5	Mandible of same; inner view	Slightly enlarged.
,,	9	5	Section of cerato-hyal of same	Slightly enlarged.
,,	10	5	Visceral arches of same, from below . .	Slightly enlarged.

List of Abbreviations.

The Roman figures indicate nerves or their foramina.

ad.m.	Adductor mandibulæ.
al.s.	Alisphenoidal region.
al.s′.	Alisphenoidal bony plate.
an.	Anus.
aq.v.	Aqueduct of vestibule.
a.s.c.	Anterior semicircular canal.
au.	Auditory capsule.
bb.	Barbel.
b.br.	Basi-branchial.
C[1].	Fore-brain.
C[2].	Mid-brain.
C[3].	Hind-brain.
d.	Dentary.
e.	Eye-ball.
e.br.	Epi-branchial.
e.eth′.	Ethmoidal bony plate.
e.o.	Ex-occipital region.
e.pa.	Ethmo-palatine.
e.pa′.	Extra ethmo-palatine.
f′.	Frontal bony scute.
fo.	Fontanelle.
g.	Gills.
h.	Heart.
h.br.	Hypo-branchial.
h.hy.	Hypo-hyal.
hm.	Hyomandibular.
hm.r.	Hyomandibular ray.
h.s.c.	Horizontal semicircular canal.
hy.	Hyoid fold.
i.hy.	Inter-hyal.
i.tr.	Intertrabecula.
iv.	Investing mass.
l.	Liver.
l.l.	Lower lip.
m.	Mouth.
mk.	Meckel's cartilage.
mn.	Mandibular fold or bar.

ms.pg.	Mesopterygoid.
mt.pg′.	Median metapterygoids.
mt.pg″.	Lateral metapterygoids.
mx.	Maxillary.
nc.	Notochord.
ol.	Olfactory capsule.
op.	Opercular scute.
o.s′.	Orbito-sphenoidal bony plate.
p′.	Parietal scute.
pa.	Palatine bone.
pa.s.	Parasphenoid.
p.br.	Pharyngo-branchial.
p.f.	Pectoral fin.
pg.	Pterygoid bone.
pg.q.	Pterygo-quadrate.
px.	Pharynx.
p.op.	Pre-opercular bone.
pr.o′.	Prootic bony plate.
p.s.c.	Posterior semicircular canal.
pt.hm.	Protractor hyomandibularis.
pt.ob.	Postorbital scute.
q.c.	Quadrate condyle.
s.ob.	Superorbital scute.
sp.	Spiracle.
sp.r.	Spiracular ray.
sq′.	Squamosal scute.
su.ob.	Suborbital scute.
sy.	Symplectic.
t.	Teeth.
t.cr.	Tegmen cranii.
tr.	Trabeculæ.
u.l.	Upper lip.
v.	Vomerine bone.
vb.	Vestibule.
v.f.	Ventral fin.
y.st.	Yolk-mass and stomach.



K.P. del. ad nat.
P. Parker lith.

ACIPENSER

West Newman & Co lith.

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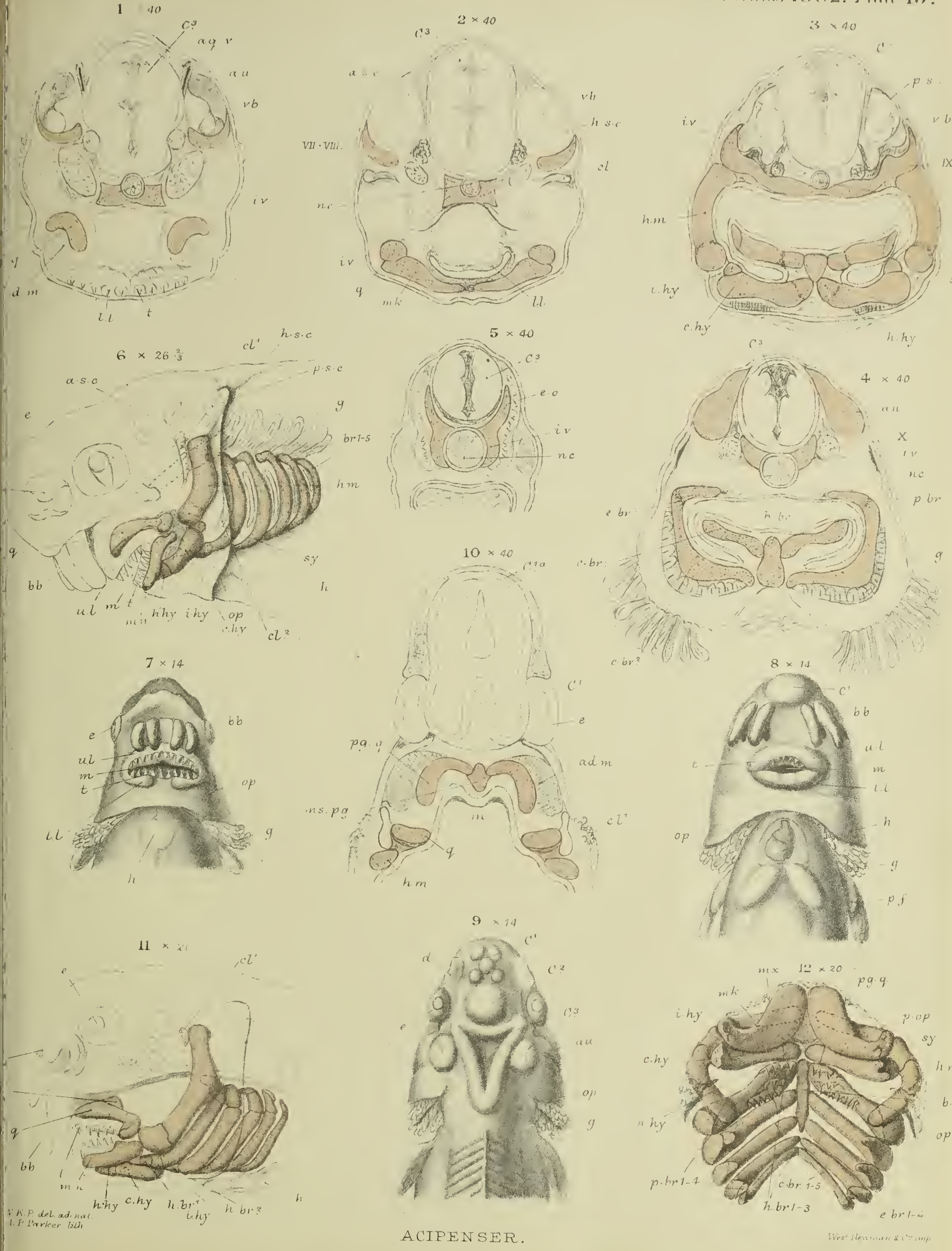

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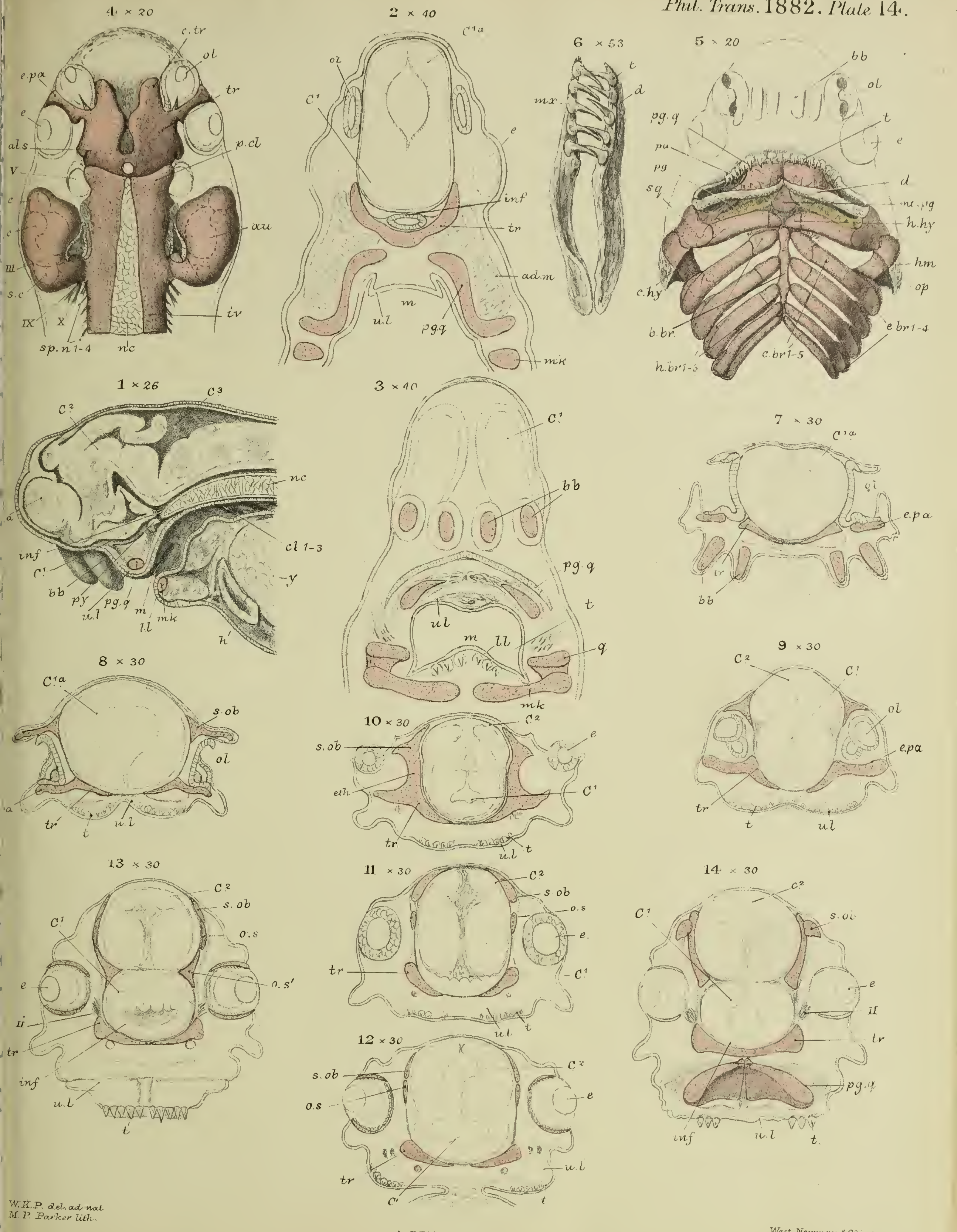

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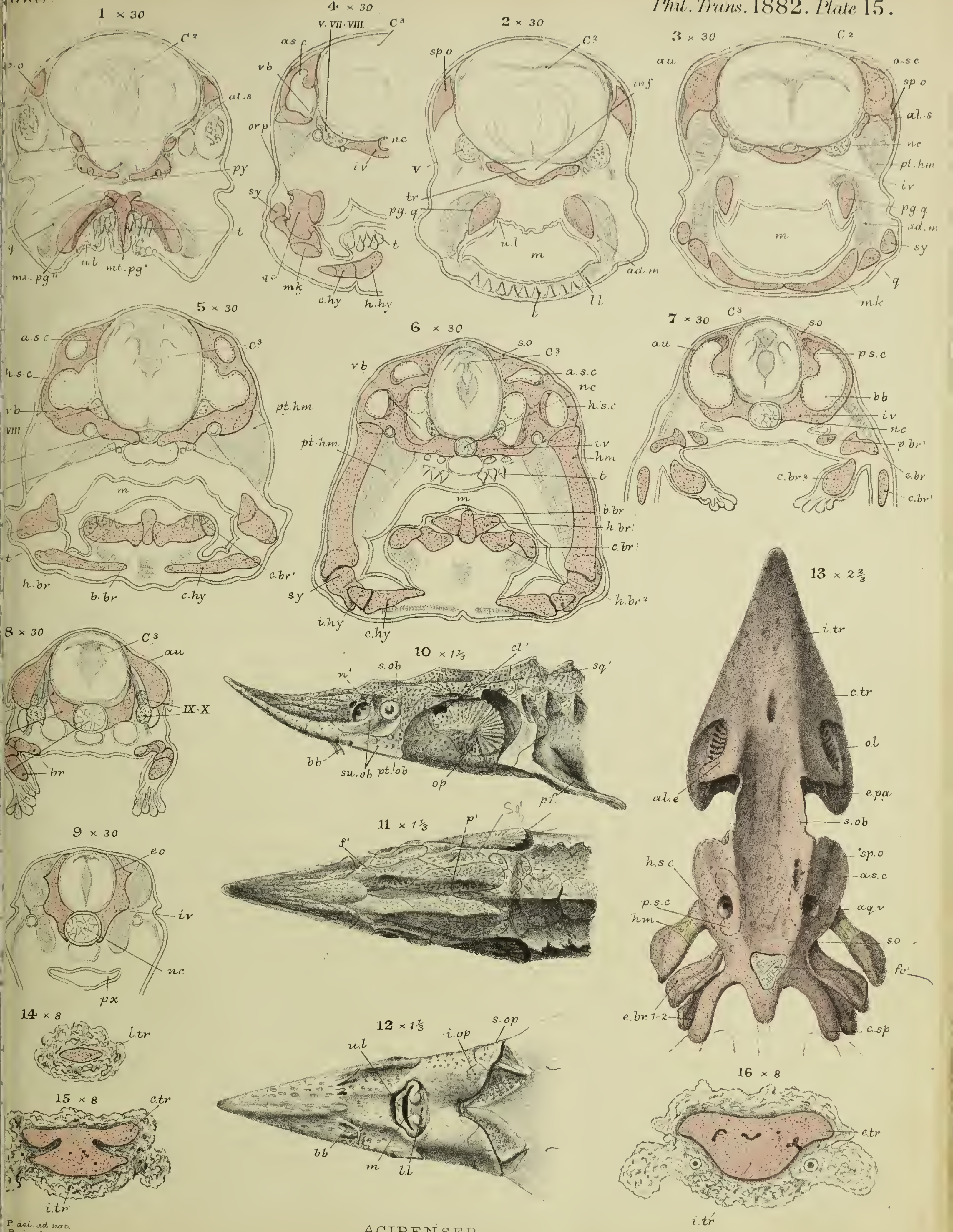

P. del. ad nat.
Parker lith.

ACIPENSER.

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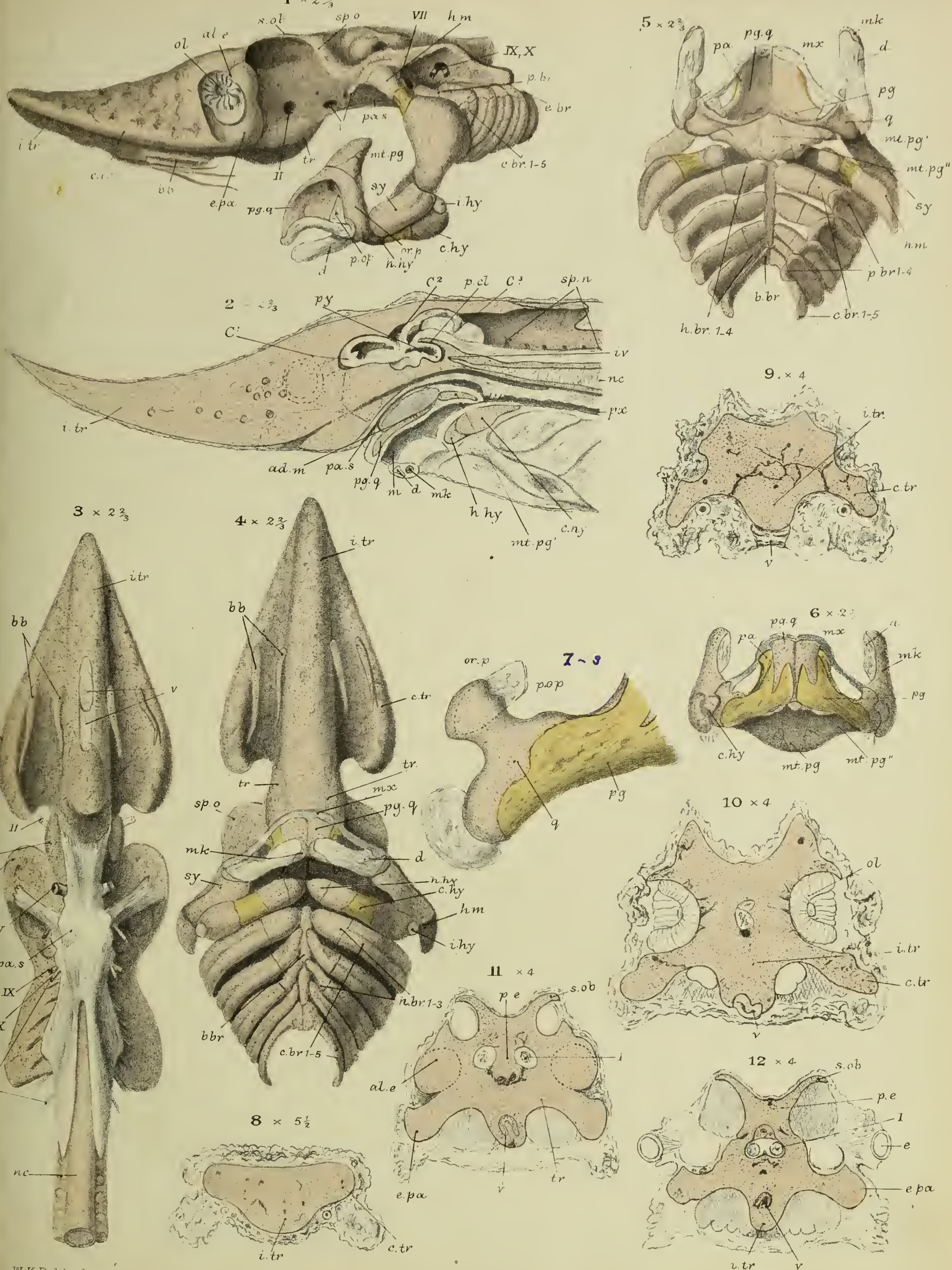

W. K. P. del. ad nat.
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ACIPENSER.

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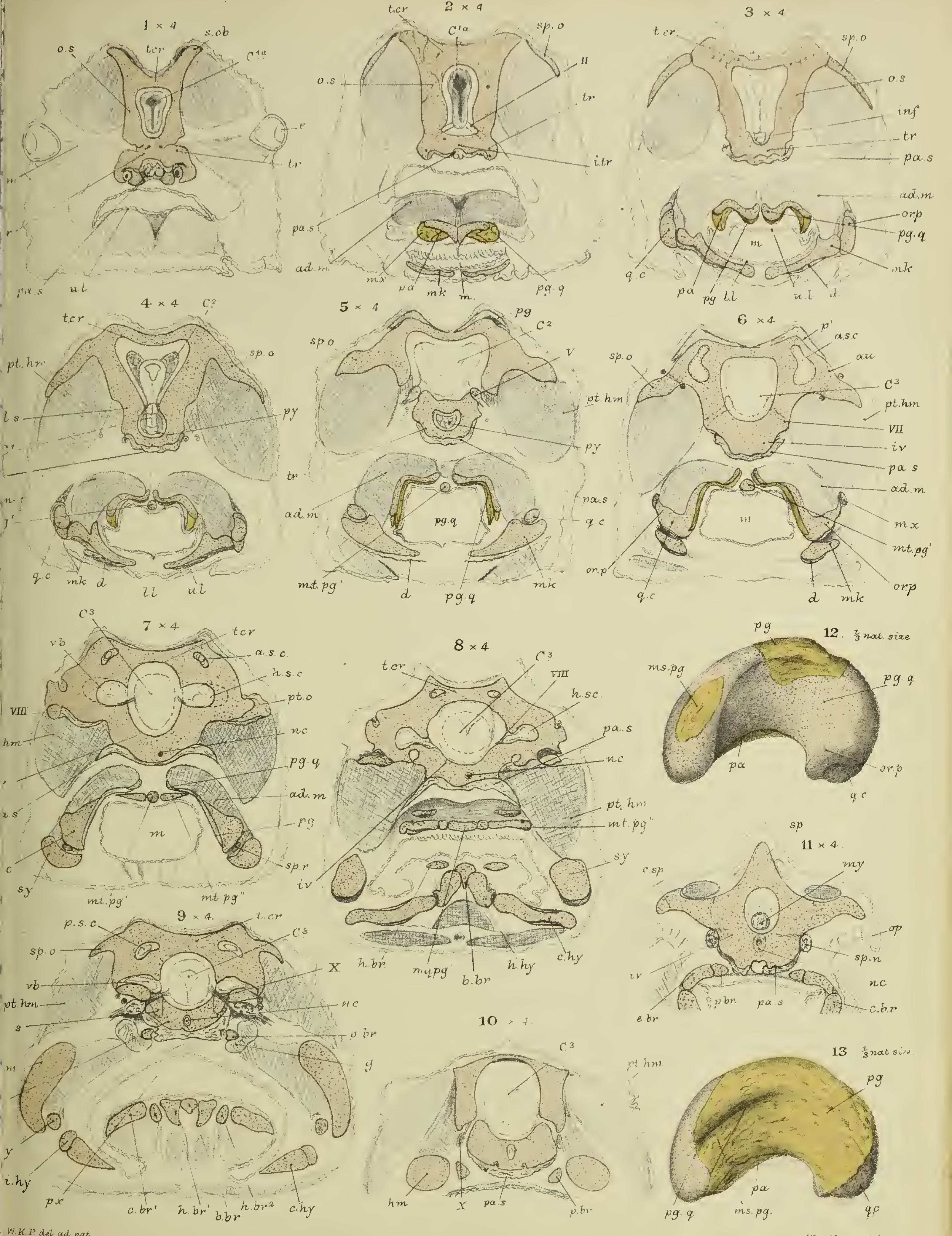

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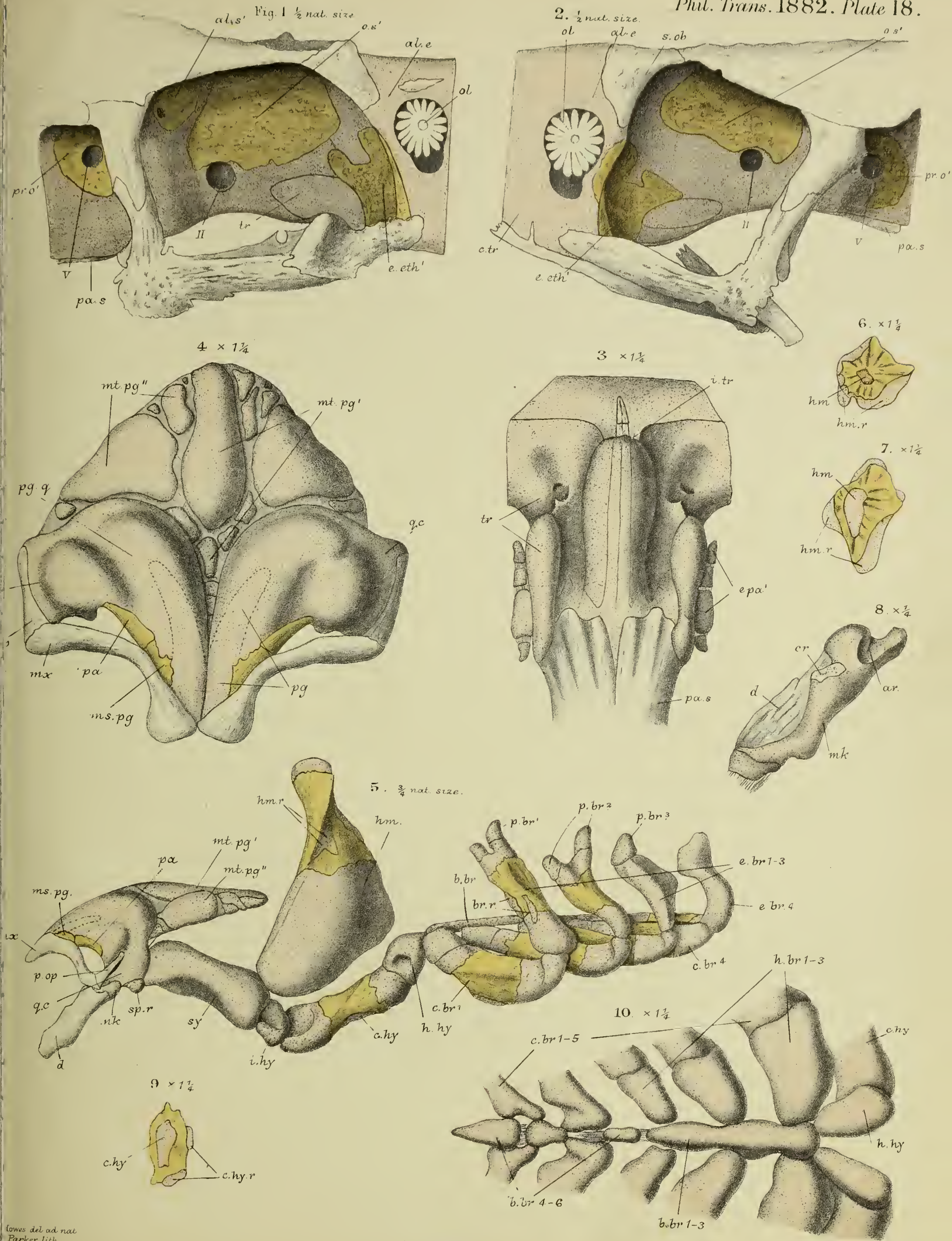
Fig. 1 ½ nat. size
al.s'
o.s'
al.e
ol
pr.o'
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ON

THE DEVELOPMENT OF THE SKULL

IN

LEPIDOSTEUS OSSEUS.

BY

WILLIAM KITCHEN PARKER, F.R.S.

From the PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY.—PART II. 1882

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VIII. *On the Development of the Skull in* Lepidosteus osseus.

By William Kitchen Parker, *F.R.S.*

Received November 3,—Read December 8, 1881.

[Plates 30–38.]

In the early part of 1879 I received from Professor A. Agassiz a large series of eggs and embryos of *Lepidosteus,* which by the help of Mr. Garman he had obtained from the Black Lake the year before. These specimens, carefully preserved in fifty-four small bottles, Professor Agassiz put into my hands to be worked out by Mr. Balfour and myself. A few years before I had received from Professor Burt G. Wilder some larger young of this Fish, which extended the "stages" for us considerably; and several adults obtained by Mr. Balfour, and one which I received from Professor Flower, made up the total of our materials. The present communication is the result of my own researches into the growth of the skull and visceral arches. Mr. Balfour, assisted by my son, Mr. W. N. Parker, has prepared an elaborate memoir on the embryology of this important type, to which are added observations on the structure of various organs in the adult.

When our work was scarcely begun I prevailed upon Dr. Traquair to work out the *adult skull,* and that piece of research is, I believe, nearly finished, so that this *Holostean Ganoid* will soon have had a fair amount of attention given to it.

My observations extend over a series of embryos and young from one-third of an inch to four and a-half inches in length. The larger young are already quite like the adult; but as Dr. Traquair's paper has not yet been sent in to the Royal Society, I shall preface mine by a short description of the adult skull: it will give the same interpretation as the promised memoir by my talented friend, for we have had several discussions upon the nomenclature and meaning of the various parts, and are of one mind as to their names and nature.

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The skull of the adult Lepidosteus.

This skull, which belongs to the long-beaked variety, is more than a foot long, and the foremost two-thirds of its length belongs to the "rostrum," which is gradually attenuated from behind forwards, and then dilates gently at the fore end. The olfactory sacs are very small, and instead of being placed close in front of the antorbital region, are carried to the end of the snout, and have on each side a pair of holes bounded by small bony plates. The orbits are a little above half an inch across, and they are bounded by a perfect "circumorbital" series. The auditory capsules are impacted into the walls of the hind skull, which at the sides is only about one-twentieth the length of the head. The occipital condyle is behind the skull; the condyles of the quadrate are in front of the orbits. There is no fontanelle in the perfect skull—that space is entirely covered by large ganoid scutes.

A. *On the superficial plates or "scutes."*

Beginning at the occipital roof, we find the hind skull covered with two large plates that represent the parietals; here, at once, we see how variable these scutes are, which answer to *much more* than the investing bones in the higher types, for there is, on the left side (in my specimen), an irregularly four-sided "dermo-occipital," the inner edge of which passes over the mid-line a little. Thus the right parietal is much larger than the left. Outside each parietal there is a somewhat smaller scute—the squamosal; this bone finishes the roof. The two or three small, irregular scutes behind the squamosal are "post-temporals," and serve as fixing-points to the *clavicular series* of the shoulder-girdle; they are post-cranial.

Outside the hinder part of the squamosal there are two smallish additional "temporal" scutes, wedged in above the "opercular."

In front of the parietals and squamosals we see the frontals; they interdigitate by large, sharp, sutural teeth, with those bones, and then run on over the orbital region, and over the hinder two-fifths of the rostrum. They are elegantly narrow-waisted (taken together) in the orbital region, and they contract into sharp styles in front, where they embrace the next pair.

These next bones are the "ethmo-nasals," or superficial splints of the ethmoidal region; they are close together along the mid line, sharp and narrow between the fore part of the frontals, and then wider; they reach, behind, within an inch and a-half of the orbits, and then run forward up to the nasals (proper). These latter are small, short, widely-crescentic plates, that lie on the small, distal, olfactory sacs; they are the *ossa terminalia* of the upper *mucous* series. The nasals finish the skull-beak above; below, an oblique transverse plate of bone supports the prenasal pad or remnant of the larval sucking-disk; it may be called the "prenasal bone." The nasal bone sends a process obliquely across the nasal opening; this bone lies in the membranous bar, which was developed early, dividing the "nostril" into two holes. Behind and under the prenasal and nasal bones we have the two short thick premaxillaries, which carry some very large, sharp teeth, as well as a rasp of smaller denticles. These bones have a palatal as well as a dentary region; and between the two the bone is punched with holes by the foremost teeth of the mandible, as in the Crocodile; the palatine processes diverge a little, behind, to embrace the vomers.

The vomers are very long, thin styles of bone, closely co-adapted along the mid line of the palatal region of the rostrum up to its hinder fourth; they have their lower face covered with a rasp of very small teeth.

Outside these there is on each side a larger splint, which reaches from the premaxillary to the antorbital space. The outside of each bone is bevelled and helps to carry the large sub-marginal teeth; these are the *superficial* palatines. Outside these, on the margin, we have the "maxillary chain" of mucous bones, about fifteen on each side, but some of them are ankylosed together; they increase in length from before backwards. The preorbital (prequadrate) space is overlapped by the last two of this chain; these are free; the larger front bone answers to the free part of the "os mystaceum" of an Acanthopterous Teleostean; the lesser scale to its jugal. A large splint passes along by its sharp fore end, on the inside of the parosteal palatine, nearly to its middle; it broadens rapidly at the prequadrate space and turns downwards, as a rounded wing. It is notched below close in front of the quadrate condyle, and then passes backwards as a large lanceolate splint, which is closely applied to nearly all the inner face of the mandibular suspensorium; this is the pterygoid bone, the osseous counterpart of the whole palato-quadrate arcade. Above the broad hind part of that arcade, close in front of the basi-pterygoid articulation, there is a much smaller lanceolate splint, the meso-pterygoid; it lies inside, but rises somewhat above the obliquely directed suspensorium. An oblong splint, rather larger than the last, lies on the outside of the lower face of the suspensorium, and is dilated where it fits to the enlargement at the quadrate condyle; this is the "preopercular": a very different bone from its counterpart in the Teleostei, and like the lower part of a Frog's squamosal. These four—the superficial palatine, the pterygoid, the mesopterygoid, and the preopercular—are the splints of the palato-quadrate arcade; the rest of the mandibular splints are on the free ramus, and will be described soon. There is a perfect "circum-

orbital" series of small, thick ganoid scutes, which run before and behind into other tracts, and are not separated as a mere ring. The upper region is composed of a chain of larger bones than the rest, and this tract is continued forwards as three bones, narrowing forwards, in the *preorbital* region, over the "prequadrate space." Behind and above, these larger bones run backwards under the squamosal until they become the "post-temporals" to which the clavicular bones are attached. They are the direct cephalic continuation of what in the Teleostei are known as the "lateral line" series. A row of small scutes runs straight down in front of the orbit from the preorbital band; the lowest of these binds on the quadrate, over the hinge, and over the foot of the preopercular. From this angular bone there is an increasing number of scutes under the orbit, and those behind the orbit become a solid tesselated pavement (part of which I have just described as lying directly beneath the squamosal), and this pavement lies on the edge of the lower part of the interopercular and covers all its ascending part.

(This most remarkable "interopercular" is much like the preopercular of the Teleosteans, and might easily be mistaken for it. It is a huge plate bent upon itself at a right angle; the ascending part is half the size of the lower region, and whilst covered by the facial "pavement," itself covers the hyomandibular and symplectic; that part is pointed above.) The lower region of the bone is a large externally ganoid tract, pointed in front, ear-shaped behind, hollow within, and coiled inwards. Behind the facial pavement, and articulated by a cup-like facet to the "opercular process" of the hyomandibular, is the opercular bone; it is four-sided, but narrow above where it articulates with the post-temporal. Its broad lower edge is toothed and overlaps the subopercular; its hind face is free and forms the upper half of the free edge of the *operculum*. The "subopercular" forms the lower half of that edge; it is a broad plate with a rounded lower and hinder margin, and is uncinate in front and above, where it is wedged in between the interopercular and opercular. These three bones—the interopercular, the opercular, and the subopercular—belong to the hyomandibular region. The splints of the mandible are ganoid where they are exposed. The main bone is the "dentary"; it covers nearly all the outside of the ramus and the upper and lower edges within. On the inside, between those edges, MECKEL's cartilage is hidden in its foremost two-thirds by a long, thin, narrow splint, the "splenial." The rami of the mandible are close together, half-way, backwards, and then gently diverge. The coronoid region is very high, large, and incurved. The "coronoid" bone flanks the front of this part as an oblique splint, and the "supra-angulare" covers the smooth, convex outside; a short, thick, wedge of bone, the "angulare," is set on to the angle of the ramus. These five bones—the dentary, splenial, coronoid, supra-angulare, and angulare—are the normal investing bones of the mandible. In the lower part of the hyoid arch there are three narrow flattened rays, from an inch to an inch and a-half in length, attached to the outer face of the "epi-hyal"; these are the "branchiostegals," and they correspond in number to what we find in the Cyprinoid Teleosteans.

Under the skull there is a long beam of bone, reaching to the middle of the vomers, lying there somewhat above them, and then escaping, showing a free keel; this is the "parasphenoid." It runs backwards, gently broadening, and then narrowing again, and gradually losing its keel, up to the "basipterygoid processes," it flanks them with a small pair of wings, and is then alate again, more extensively, under the "sacculus" of the ear, and ends as two flat processes under the basioccipital, and nearly reaching to its end.

B. *On the endo-cranial bones.*

In the hind skull I fail to find a distinct supraoccipital under the roof, for the exoccipitals meet there, and are separated only by a narrow tract of cartilage. The basioccipital is large, and projects beyond the arch; its hollow articular face is transverse, and notched above and below. The exoccipitals are large, and finish the arch above. The auditory capsule is invested by *four* cartilage bones on each side, viz.: a large prootic, a middle sized epiotic, and a small opisthotic, and the sphenotic bone which is of the average size, and ossifies the post-orbital angle of the endocranium, where the fore part of the auditory capsules are imbedded. I can find no "pterotic" under the squamosal. There are two alisphenoids, and they ossify the basipterygoid processes, but I find no distinct basisphenoid, presphenoid, nor orbito-sphenoids; although after the brain cavity has retreated, losing much of its front part, a bony plate is found in the presphenoidal region. This plate is thin, fenestrate, and rests upon the parasphenoid. I believe that it is formed by the coalescence of the once distinct lateral ethmoids, which were at first formed in the sides of the fore part of the chondrocranium, like the primary elements of the Frog's "girdle-bone" (see Plate 38, figs. 2, 3, *l.eth.*). The rostral part of the endocranium is, I believe, unossified, even in the adult.

The quadrate and metapterygoid bones occupy only part of the mandibular suspensorium; the rest remains unossified; the metapterygoid bone takes up the part which answers to the pedicle and rudimentary otic process; a facet of cartilage covers it where it articulates with the "basipterygoid process." The hyomandibular is fenestrate and well ossified; it is only half as large as the mandibular suspensorium. A short tract of cartilage separates its upper from the slender long symplectic.

The articulare is a strong solid mass of bone, capped by a saddle-shaped condyle for articulation with the quadrate.

The small inter-hyal piece is not ossified, but the epi-, cerato-, and hypo-hyals are; the long *double* basi-hyal ("ento-glossal") does not become solid bone, but it is *endosteally* hardened. The fore part of the basi-branchial series is slightly ossified, the arches are as well ossified as in the ordinary Teleostei; thus there are in the first four arches a pharyngo, epi-, cerato-, and hypo-branchial piece, largely converted into bone; the fifth is ossified, but it only has the cerato-branchial element in it.

First Stage.—Recently hatched young of Lepidosteus, $2\frac{3}{4}$ *to* $4\frac{1}{2}$ *lines long.*

At this stage (Plate 30, figs. 1, 2) the mesocephalic flexure is at its fullest development, but the angle formed by the meeting of the *para*-chordal and *pro*-chordal regions is very open. Moreover, the bend appears less than it is, for the snout is very large and dilated, and its axis is coincident with that of the cerebral hemispheres (C^{1a}.) and of the mid brain (C^2.).

The fissure, however, between the fore and hind brain (C^3.), and below the mid brain, is very large, and is turned backwards considerably, above; the notochord (*nc.*) seeks to ascend into this space, but only rises one-third of the way to the top; the third nerve descends in this cavity to reach the orbital muscles.

In the sectional figures given to illustrate this stage, very little of the primordial cranium comes into view; it is not yet formed into consistent cartilage, but the "embryonic cartilage" is sufficiently developed to show the cranial and facial rudiments.

The pituitary body (*py.*) is distinguishable from the palatal skin, and it is quite free above, the infundibulum (*inf.*) lying over it.

In both figures (Plate 30, figs. 1 and 2, cl^{1-4}.) the clefts and visceral folds are visible on their inner or *hypoblastic* aspect; in the more advanced specimen a rod of solidifying tissue was seen as cut through in six of these, namely, the mandible, hyoid, and four of the branchial arches (*mn.*, *hy.*, br^{1-4}.)—all but the *fifth*, which remains rudimentary.

The heart (*h.*) is seen impacted between the mandibular rudiment (*mn.*) and the yolk (*y.*); it thus lies as far forwards as the snout.

The notochord (*nc.*) is very large, and in the more advanced specimen (Plate 30, fig. 2) the terminal hook of this cephalic end of the rod is fixed in between the infundibulum (*inf.*) and the swelling antero-inferior part of the hind brain (C^3.).

Second Stage.—Recently hatched young of Lepidosteus, 5 *to* $5\frac{1}{2}$ *lines long.*

In somewhat larger specimens (about 11 millims. long) I was able to make preparations of the whole chondrocranium (Plate 30, fig. 3): a sectional view is given of a somewhat larger specimen (Plate 30, fig. 4).

The section shows that the skull is rapidly straightening, but of course the great *clinoid fissure* is never obliterated. This is formed by the primordial flexure, and is always permanent in the Vertebrata; but the flexure itself is not so great in this type as in the *Amphibia* and the "Amniota."

The notochord (Plate 30, fig. 4, *nc.*) is not traceable so far up in the clinoid region as it was; the pituitary body (*py.*) is still independent of the infundibulum (*inf.*).

In the dissected skull (Plate 30, fig. 3) the basal and facial parts alone are chondrified, the sides and roof are entirely membranous; the cartilage is still very fragile, but quite differentiated from the surrounding connective-fibre cells. The chondrocranium

proper is at present composed of two bands of cartilage, which run from the atlas to the large suctorial snout (*s.d.*); the lateral structures are the auditory capsules and the visceral arches.

The basal pair of bands (Plate 30, fig. 3, *iv.*, *tr.*) are thickest behind and at the fore end; for two-fifths of their length they embrace the notochord by their inner edge; they then diverge from each other so as to form a large spindle-shaped space (*py.*) in front of which, for an eighth of their whole length, they approximate, but do not come into contact with each other.

These dilated fore ends of the basal bands are as broad as the parachordal part behind (*iv.*), but are not so thick; they are conjugated by a tract of embryonic cartilage, the rudiment of the "intertrabecula" (*i.tr.*); they themselves are the rudiments of the cornua trabeculæ (*c.tr.*). The bowed interorbital part of the basal bands are the trabeculæ (*tr.*), they are only half the width of the hind and fore parts; these out-bent bars do not merely fence in the small pituitary body, they embrace the base of the fore-brain.

The free, ascending, blunt end of the cranial notochord (*nc.*) is twisted a little to the left—it may curve either way, but the appearance is partly due to artificial pressure; it is not invested by a large ascending "posterior clinoid" cartilage, as in the *Amniota*, for that tract is very small and very late in appearance in *Lepidosteus*. The *pro*-chordal part of the basal bands is bent somewhat upon the *para*-chordal part. Behind the exit of the 9th and 10th nerves and the hind face of the auditory capsules the investing bars (*iv.*) thin out, and end in a sharp edge in front of the 1st vertebra.

The auditory capsules (*au.*) are of a short oval shape; they are largely chondrified, but the layer of cartilage is very thin; below, there is an oval fenestra, still membranous (*au.f.*); it is about two-fifths the length of the capsule. The capsules and the investing bars are only connected together by embryonic cartilage at present; the convexity of the capsules has produced a corresponding concavity in the side of each bar. The horizontal canal bulges over the lower convex part, which contains the otolith; thus there is a rudimentary "tegmen tympani." Rudiments of all the framework of the visceral arches are now present, but the segmentation of these parts is imperfect. The skeleton of the first and second arches—mandibles and hyoid—is massive; that of the branchial arches is very delicate. The pier of the mandibular arch (*p.pg.*, *q.*, *pd.*) is not a mere "pterygo-quadrate," as in the Selachians, Teleostei, and Urodeles, but is a "palato-quadrate," as in the Anura. This arises from the primary continuity of the ethmo-palatine cartilage with the pterygoid fore-growth of the mandibular suspensorium; and this is not all, for the *palatine region* of the bar is also *primarily continuous* with the trabecula at its dilated fore end.

The "pedicle" of this compound suspensorium is not *fixed*, as in the Tadpole, but *free*, as in the metamorphosed Frog; as soon as it is sufficiently developed to articulate with the basal bar, it will then, at that part, correspond very accurately with what we find in the adult Frog. At present this palato-quadrate, or suspensorial cartilage is

roughly scythe-shaped, the "blade" being behind, and lying between the auditory capsule and the narrowing basal band, whilst the "handle" is in front, and is glued to the trabecula. The blade is shorter than the handle, and on its heel it has an oval, condyloid facet, which looks forwards and a little outwards and downwards ; it is pinched a little behind this facet, and then becomes an apiculated lanceolate blade. The handle is oval in section, narrow at first, and then wider as it turns inwards at its junction with the trabecula. A free bar, rather shorter than the "handle," and having its thick end reversed, or behind, articulates by a flat facet with the flat facet of the suspensorium. This is MECKEL'S cartilage, or the free mandible (*mk.*).

Already, in the coronoid region, this short lower jaw is elevated into a crest; its lower edge is convex, its upper concave, and its end is blunt ; it reaches nearly as far forwards as the palatine region of the suspensorium. Between the convex hind margin of the first arch (suspensorium and mandible) and the concave fore margin of the next (the hyoid) arch there is a *hypoblastic pouch* (see Plate 30, figs. 1 and 2, cl^1.), but this first cleft does not open on the outside, like the hyo-branchial and four branchials.

The hyoid arch consists already of *four* segments on each side, with the rudiment of a median conjugating bar, composed of embryonic cartilage. The pier (*hm.*) of the hyoid arch, like its counterpart in the Mammal, is anvil-shaped ; this is the hyomandibular, with its symplectic process, the counterpart of the pterygoid fore-growth of the mandibular pier or suspensorium.*

At present it is only a fourth less than the pier in front of it; but it becomes relatively much less, instead of much larger, as in the Teleostei. The hyomandibular is now a solid mass of cartilage, concave above, bilobate below, and sending upwards, to the auditory capsule, a thick process, and downwards, to the articular process of the suspensorium, a sharp process. The upper process is its proximal part or head, the lower is its symplectic prolongation.

The middle part has two lobes, below, and behind ; the upper of these afterwards gives off the opercular process, the lower is already scooped on its inside where it articulates with the next joint, the inter-hyal (*i.hy.*). This latter piece is a small pyriform segment, with its lesser end upwards and hooked inwards, for articulation with the hyomandibular. This is, so to speak, a supernumerary segment placed between the *antero-superior* pier and the *postero-inferior* arch. That arch is already composed of a main bar above, the cerato-hyal (*c.hy.*),—a thick rounded rod, and a short, almost globular segment below, the hypo-hyal (*h.hy.*); the two fit together by flat facets ; the right and left hypo-hyals touch each other below. In front of and between these lower segments there is a tract of tissue which will harden into the basi-hyal (*b.hy.*).

The branchial arches (*br.*) are slender rods, bent in a sigmoid manner so as to form round in-turned hooks, above. The last (br^5.) is only one-fourth as large as the other

* Mr. BALFOUR informs me that this bar is primarily continuous with the skull, and that after chondrification it is still unsegmented.

four, and is permanently arrested as the "inferior pharyngeal;" it is simply a short cerato-branchial.

The four well-developed rods are not yet segmented across into the normal pieces; they are oval in section, pointed above, and rounded below, where they articulate with the common basi-branchial (*b.br.*), which is one-third thicker than the arches. This conjugating rod is somewhat flat; it is thickest in front, where it fits by a rounded end between the hypo-hyals, and flat behind, where it projects beyond the arches.

Third Stage.—Young Lepidostei, $7\frac{1}{4}$ *to* 8 *lines long.*

In young individuals about two-thirds of an inch (16 to 17 millims.) long, the cartilage has become quite consistent, and some parts not chondrified in the last stage have become solid.

The head (Plate 30, figs. 5, 6) has straightened out considerably, and the basis cranii bulges below; but the sharp, recurved fold under the mid brain, where the fore and hind brain approximate, although a mere chink, is ineradicable.

The round and curiously mammillated snout is much smaller now, relatively; the notochord (*nc.*) has retreated considerably; the pituitary body (*py.*) is still separate from the infundibulum (*inf.*).

The azygous trabecular bar (figs. 7, 8, *i.tr.*) now shows itself in sections taken vertically through the head, but all the rest of the basal cartilage is far from the mid line. The notochord (*nc.*) is very large, and descends considerably beneath the swelling hind brain (figs. 5, 6, C^3.). Below the mouth and throat, the fore end of the mandible is seen in the *right* section (Plate 30, fig. 5, *mk.*); it contained more than half of the head above, and less than half below; thus that rod, and the rest of the post-orals (*hy.*, br^{1-4}.), are cut through a little on the right side of the middle. But in the *left* half (Plate 30, fig. 6), the median rods (*b.hy.*, br^{1-4}.) are brought into view, below; above, the junction of the trabecula with the palato-quadrate (*tr.*, *p.pg.*) is seen; this, however, had to be exposed by dissection; the sub-ocular space is seen as a crescentic gap with its convexity downwards.

The chondrocranium is figured as seen from above and below in a dissection of a somewhat larger specimen (8 lines long); it is much more perfect than in the last stage (Plate 30, figs. 3, 7, 8).

A full third of the cranial floor is membranous; the side walls are membranous in front, and are made by the auditory capsules behind; but a rudiment of the roof or "tegmen cranii" is now found, right and left.

The thick cranial notochord (*nc.*) is only half the length of the chondrocranium, now; it is somewhat moniliform, lessening by three successive stages, and is bent a little in this specimen to the right.

The narrow part is rounded at its end, and ascends but little into the clinoid fissure (Plate 30, fig. 5, *nc.*); a third part at least is not invested by the parachordal cartilage (*iv.*).

The huge so-called pituitary space (*py.*) is pyriform, has an indented outline behind, and is apiculate in front. The concave inner side of the basal bands embrace the notochord closely, and end behind in bevelled flaps; in front, where the last narrowing of the notochord takes place, they end almost transversely, but give off from their outer edge the trabecular outgrowths. They are quite confluent, externally, with the well-chondrified auditory capsules (*au.*). In their broad, proximal part the trabeculæ (*tr.*) are dilated, and are perforated by the internal carotid artery;* thence they converge steadily as scarcely arcuate bands, only one-third as large as their parachordal roots (*iv.*).

Their front confluent part is as long as their hinder separate part; and there the bands double their width, have a convex outline externally, and narrowing inwards at their extremity, are continuous then with the palato-quadrate bars (*p.pg.*). The front margin of these four bands is crenate, with three convexities, the middle enlargement being the largest; this is not, however, formed by the trabeculæ themselves, but by a pyriform wedge of newer cartilage, which has developed between and above them. This new element is the intertrabecula (*i.tr.*); in the last stage (Plate 30, fig. 3, *i.tr.*) it was merely composed of embryonic cartilage—a small, inconspicuous tract of tissue, lying between the dilated ends of the trabeculæ (*tr.*).

This new tract does not reach to the pituitary space, but already, in the upper view, can be seen projecting beyond the confluent paired bands (*tr.*, *p.pg.*). The simple, ovoidal form of the auditory capsules (*au.*) is now lost, for the semi-circular canals (*a.s.c.*, *h.s.c.*, *p.s.c.*) have developed greatly, and they have given the form of their curves and swellings to the cartilaginous capsule.

The floor of the sacculus is still largely membranous (fig. 7, *au.f.*); this circular fenestra is inside the centre of the floor; within, also, the capsule is not cartilaginous. Outside, the bulging of the horizontal canal (*h.s.c.*) has formed a rudiment of the "tegmen tympani" (fig. 7); this, however, is simply used to form the large oblong concavity for the hyomandibular (*hm.*), and never acquires any tympanic function.

The large cranial nerves have free course over the basal plate, and in front of and behind the auditory capsules they have only membrane to pass through; the space for these (Plate 30, figs. 7, 8, IX., X.) is seen to be very wide.

From the front of the auditory capsule cartilage is creeping along the superorbital region (fig. 8, *s.ob.*); this new tract is styliform, and at present only reaches one-third of the distance to the end of the chondrocranium. Below this rudiment, right and left, of the "tegmen cranii" the proximal part of each trabecula has developed an oblong facet of cartilage for articulation with the *pedicle* of the suspensorium (*pd.*); this is the first appearance of the paired "basipterygoid" processes of the basicranii. I take this to be not only the first appearance of these important processes in

* This passage is seen inside the superorbital cartilage (*s.ob.*); the line leading from the letters to this part in fig. 8 is not long enough.

the development of this particular skull, but also in the order of the types; in the Amphibia, Reptiles, Birds, and Mammals these processes are seldom absent.

The dorsal end of the suspensorium or mandibular pier has already become oblique; the true extremity is now lateral, and is the pedicle of the pier; this is an oblong tract or facet articulating with the basi-pterygoid face on the basal band.

The second part is the otic process (behind *pd.*); it is a subtriangular "ear" of cartilage, running backwards towards the pier of the hyoid arch (*hm.*), under the superorbital rudiment (*s.ob.*). Thence the suspensorium narrows gently, and a little behind the middle of the bar forms, on its outside, a jutting step; this is the gently concave quadrate hinge which articulates with the mandible (*mk.*).

The rest of the suspensorium lessens to one-half its hinder width, and is *f*-shaped, bending inwards at first and then outwards before it makes its last inward bend to join the trabecula (Plate 30, figs. 7, 8, *p.pg.*, *tr.*). The extent of the coalesced part is greater than the width of the bar; both that part and the fore part of the free bar belong, not to the proper pier of the mandible, but to the palato-maxillary arcade—it is the proper "ethmo-palatine." In the Tadpole of all, and the adult of most, Batrachia, it is not differentiated from the pterygoid band. The mandible (*mk.*) has already a flattish articular facet, an angular and a coronoid process; the main bar is gently arcuate, and lessens gradually to its distal end, which is rounded, and does not touch its fellow of the opposite side.

The hyoid arch is large and highly subdivided; it has now a large forwardly-projecting basal piece (Plate 30, fig. 8, *b.hy.*).

The pier is the hyomandibular (*hm.*), with its styloid symplectic fore-growth (*sy.*); this part is free, and not, like its serial homologue the pterygoid process of the suspensorium, concrescent with the bar in front of it. This hyoid pier is still three-fourths as large as the pier of the mandible; its dorsal condyle is large and rounded, its body is swollen behind, ready to form the "opercular process," and below this knob, on the inner side, it is scooped for articulation with the inter-hyal (*i.hy.*). Here, as in the *hyostylic* types of fishes, the hyoid arch is subdivided primarily into an antero-superior and a postero-inferior bar; but in this type, as in the Teleostei, the latter is subdivided again into three segments—the inter-hyal, the cerato-hyal, and the hypo-hyal (*i.hy.*, *c.hy.*, *h.hy.*).*

The inter-hyal (*i.hy.*) is a small, short, but thickish segment which articulates with the inner face of the hyomandibular (*hm.*) above, and with the cerato-hyal (*c.hy.*) below. The cerato-hyal is nearly as long as the mandible, and is twice as thick as its distal part; it is oval in section, rather pinched in at the middle, and rounded at both ends. The lower convex end fits into the shallow cavity on the top of the hypo-hyal

* In the Sturgeon and its congeners the symplectic is segmented off from the hyomandibular, and the same thing often occurs in the diminished and modified hyoid pier of the Batrachia, and even amongst some of the *Sauropsida*, as in the Chelonia (see 'On the Skull of *Chelone viridis*,' "Challenger" series, vol. i., part 5, plate 6, figs. 6, 6*a*).

(*h.hy.*), the thick, semi-globular, distal segment of the arch. The basal piece, *glosso-* vel *basi-hyal* (*b.hy.*), is wide, oblong, and three-fourths the height of the cerato-hyal; its rounded fore end is rather blunt; it is, in reality, a double bar, and its tissue is much lighter and more spongy than that of the side bars; its posterior end is doubly scooped for articulation with the hypo-hyals.

The branchial arches (Plate 30, fig. 8, *br'.*) are now beginning to divide across into four pieces on each side, namely, a pharyngo-, an epi-, a cerato-, and a hypo-branchial (see Plate 31, figs. 12, 13); a rod of cartilage of about the same thickness as the arches runs along the mid line, connecting them together; this is the basi-branchial (*b.br.*).

Transverse sections of a somewhat younger specimen ($7\frac{1}{4}$ lines long) show much that is instructive, and corroborate the observations made upon *dissected* embryos.

Section 1.—The first of these (Plate 31, fig. 1) is in front of the chondrocranium, through the fore part of the nasal capsule (*ol.*). The skin is very thick, and the mucous membrane of the nasal sac is composed of large columnar cells. The upper part is much flatter than the lower, in which three of the suctorial disks (*s.d.*) are seen in section.

Section 2.—The next section (Plate 31, fig. 2), is through the middle of the nasal sacs (*ol.*) and the fore-part of the hemispheres (C^{1a}.); here the lower face is less convex and the upper more so; the fore end of each trabecula (*c.tr.*) is cut through; it is a rounded projection, the rudiment of the free cornu.

Section 3.—The third section (Plate 31, fig. 3) is through the back of the nasal sacs (*ol.*), the first third of the cerebral hemispheres (C^{1a}.), and the solid coalesced end of the triple trabecular outgrowths of the basis cranii. The outline of the trabeculæ (*tr.*) is clearly seen below; but above, these bars—which are oval in section at this part and very thick—are confluent with an upper median mass, the intertrabecula (*i.tr.*); this is wider than the paired bars, fits in and on them, and rises over them as a dilated and concave floor to the membranous floor of the cranium.

Section 4.—The fourth section (Plate 31, fig. 4) is through the hemispheres (C^{1a}.) and barely misses the eye-ball (for *ol.* read *e.*). Here the fore end of the palato-quadrate cartilages (*p.pg.*) is cut through, where these bars run into the trabeculæ (*tr.*). The intertrabecula (*i.tr.*) is wider and flatter, and the shallow sulcus between the paired trabeculæ is gone; they together form a convex mass below, at this part. The section of the palatines would be circular, but the conjugational band is very thick, and obscures their real form.

Section 5.—The fifth section (Plate 31, fig. 5) runs through the fore part of the eye-balls (*e.*). This section is at the end of the intertrabecula (*i.tr.*), and the trabeculæ and palatine bars (*tr.*, *p.pg.*) are only half as large as in the last, and this section is seen to be oval, for the connecting cells are much reduced in quantity.

Section 6.—The sixth section (Plate 31, fig. 6), a little farther back, shows an evident fissure between the trabeculæ (*tr.*), which are now flatter, like bricks, and the connecting band is so thin as almost to set the palatine band (*p.pg.*) free.

Section 7.—Here (Plate 31, fig. 7) those bands (*p.pg.*) are free, and the trabeculæ (*tr.*) look like two flat, partly confluent bricks, gently bent round the base of the membrano-cranium. The section of the palatine bars, now very slender, is circular.

Section 8.—In this section (Plate 31, fig. 8) the eye (*e.*) is cut through its middle, and the mandible, very short as yet, has come into view; here, of course, the mouth cavity (*m.*) is shown. The pineal body (*pnl.*) and the fore part of the mid brain can just be seen, as well as the back part of the hemisphere (C^{1a}.), running into the thalamencephalon below. The trabeculæ (*tr.*) do not now follow the convexity of the membrano-cranium, but are flat and horizontally placed; they are distinct here, and oval in section. The palatine bars (*p.pg.*) are now round in section, and are more than twice their own diameter from the trabeculæ. Below the mouth cavity (*m.*) the mandibles (*mk.*) are cut through obliquely; they are rounded rods, similar to the palatines at the same part.

Section 9.—The ninth section (Plate 31, fig. 9) is through the mid brain (C^2.) and the thalamencephalon (C^1.). The trabeculæ (*tr.*) are now nearly cylindrical, and are a distance apart equal to twice their own thickness. Between them a thin lamina of bone is cut through; this is the parasphenoid (*pa.s.*). Outside the oral cavity (*m.*) the palato-quadrate cartilages (*p.pg.*) are seen to be flattened and concavo-convex, the convex side being turned inwards. On each side, below the mouth, the mandibles (*mk.*) are cut through obliquely. Above, in the superorbital region, the rudiment of the tegmen cranii is seen as a narrow band of cartilage—flat outside and convex within.

Section 10.—In the next section (Plate 31, fig. 10) the swelling mid brain (C^2.) reaches the superorbital bands on each side; the trabeculæ (*tr.*) are nearly twice as far apart as in the last, and are quite circular in section. Between and below them the parasphenoid (*pa.s.*) is twice as wide as in the last. This section shows the articular end of the mandible (*ar.c.*) joined to the hinge on the quadrate end (*q.*) of the palato-quadrate pier; this part is now high, flattened, and convexo-concave, with the concavity on the outside.

Section 11.—This is through the widest part of the mid brain (Plate 31, fig. 11, C^2.), the thalamencephalon (C^1.), the infundibulum (*inf.*), and the distinct pituitary body (*py.*). The superorbital bands are flatter and nearly vertical in position; the trabeculæ (*tr.*) are now furthest from the mid line; the parasphenoid bone is still visible below the pituitary body; and the convexo-concave quadrates (*q.*) are now cut through *behind* the mandible at the mid line below the mouth (*m.*). The tongue (*tg.*) is cut through in front of its cartilaginous core.

Section 12.—The next slice is through the hind brain (Plate 31, fig. 12, C^3.), the front part of the auditory capsule (*vb.*), and the fore end of the notochord (*nc.*). On each side of the hind brain there is a large mass of nerve-cells, the rudiment of the ganglia of the trigeminal and facial nerves (V., VII.).

The investing mass (*iv.*), wide up to its fore end, and not embracing the ascending apex of the notochord (*nc.*), is a rather thick plate of cartilage; the inner edge of each

slab does not touch the notochord at this part. These basal bands are quite confluent with the auditory capsules, which are very solid on their outer side, but remain membranous to a considerable extent on the inner.

The anterior semicircular canal (*a.s.c.*) is cut through, and also the main cavity (*vb.*) with the horizontal canal opening into it; this canal bulges out the capsule, and under the "tegmen" thus formed we see the hyomandibular (*hm.*) as a continuous ray, thick and bulbous, below. Below it, at a little distance, the joint being further back, we see the second segment, or inter-hyal (*i.hy*); it is short and semi-elliptical, with a truncated end below. That end articulates with the rounded top of the phalangiform cerato-hyal (*c.hy.*), which is between it and the hypo-hyal; this latter segment was in front of this section (see Plate 30, fig. 8, *h.hy.*)

The foremost branchial arch is cut through near its ventral end, through the lower part of the cerato-branchial, as well as the distil and basal pieces (*c.br.*, *h.br.*, *b.br.*); these parts lie behind the tongue.

Section 13.—The next section (Plate 31, fig. 13) is behind the junction of the auditory capsules with the basal plates. These latter are here very massive, and almost square; the notochord (*nc.*) between them is very large; the ganglia of the vagus and glosso-pharyngeal (IX., X.) fill up much of the space below, between these bars and the capsules; but above, the open space is for the auditory nerve (VIII.). The anterior and posterior canals (*p.s.c.*) are cut through at their junction, and the horizontal canal where it opens behind into the vestibule (*vb.*). The hyomandibular (*hm.*) is severed behind its upper, or articular head, and that is the only part of the hyoid arch which comes into view here. The lower part of two of the branchial arches (*br.*) is cut through close above the heart (*h.*).

Bony matter is forming in the opercular fold, a growth from the hyoid region, and its great size, wrapping over the gill-arches and heart (*h.*), is well shown.

Section 14.—In this section (Plate 31, fig. 14*), the auditory capsule is seen to approach the investing mass (*iv.*) behind the large membranous deficiency in the inner wall. The basal plates cut through are here at their thickest part, and the posterior canal (*p.s.c.*) is most of it seen, as it becomes bulbous below. Here the notochord (*nc.*) has almost its full (*spinal*) thickness; the hyomandibular is cut through in its hinder part, or "opercular process;" only the upper part of this section is figured.

Section 15.—This (Plate 31, fig. 15*), which is behind the ear-capsule, shows that the occipital ring is still very incomplete, only the basal and lateral parts (*e.o.*) being developed. The basal cartilage (*iv.*) is thinning out towards the first vertebra; the pharyngo-branchial of the last functional arch (*p.br.*) and its gills (*br.p.*) are displayed; the notochord (*nc.*) is now full-sized. A comparison of these sections with the upper and lower views of the chondrocranium at this stage (Plate 30, figs. 7, 8) will make all plain.

* Fig. 14 is lettered 15, and fig. 15, 14 by mistake.

Fourth Stage.—Young Lepidosteus, $11\frac{1}{2}$ *to* $12\frac{1}{2}$ *lines long: average size* 1 *inch.*

In these, the largest of those reared by Professor AGASSIZ and Mr. GARMAN, the chondrocranium is perfect ; the occipital arch is beginning to ossify, and the investing bones are very numerous and quite distinct.

The cranium at this stage (Plate 32) corresponds very closely with that of a young Sturgeon *five inches* long, but has much larger membranous tracts, and is altogether a much lighter structure; in having rudimentary basi- and ex-occipital bony centres, it has already gone beyond the skull of an adult Sturgeon.

The fissure between the fore and hind brain (Plate 32, fig. 4, C^1., C^3.) is very distinct, and reaches to the base of the mid brain (C^2.); but there is no "posterior clinoid wall," such as would exist and be very massive in the skull of an embryo Sauropsidan or Mammal at the same stage.

Already the notochord (Plate 32, fig. 4, *nc.*) has retreated to a considerable distance behind the pituitary body (*py.*), which is now an appendage to the infundibulum (*inf.*); the brain well fills the whole cranial cavity up to this stage, but the hemispheres (C^{1a}.) are relatively very small.

Another thing to be noticed is this, namely, that the *pre-cerebral* growth of cartilage is almost as long as the whole cranial cavity, although it is only a fraction of the length to which it will attain. At first sight it might be thought that the mesocephalic flexure was gone, but the up-throwing of the mid brain, and the meeting of the fore and hind brain, show that the bend is very large and very sharp *at one point.* The four faces of the skull are all largely membranous, and but for the notochord (*nc.*), the floor would be open along nearly its whole length, for the cartilage only closes in at the mid line beneath the front end of the hemispheres and the olfactory lobes (C^{1a}., C^{1b}.). The thick cranial notochord (*nc.*) is receiving a bony investment between the thin, post-auditory ends of the investing mass (*iv.*); this will be seen better in the transverse sections (Plate 33). The fore ends of the basal bars (figs. 2, 3, *iv.*) diverge from the notochord (*nc.*) some distance behind its apex ; in the middle part they are completely confluent with the auditory sacs.

The narrowed, diverging bars that retreat from, and then shoot on far in front of the notochord, are the trabeculæ (*tr.*); they approximate gently, and their interspace in front is sharply pointed. But the trabeculæ have not merely approximated, they are united together by the intertrabecular wedge (see Plate 31, figs. 7, 8, *i.tr.*); and this has now become a large rod, running forwards to the end of the narrow snout.

Outside this thick rod, but little of which is formed by the lateral bars, those bars grow externally into a large lanceolate leaf of cartilage, which reaches right and left nearly to the small, *distant* nasal sacs (fig. 5, *ol.*). These peculiarly *Acipenserine* outgrowths of the trabeculæ are the familiar "cornua" (*c.tr.*) curiously modified ; both ends of each leafy growth are free, as rounded ears of cartilage; on the inside there is a sulcus, deepest, on both surfaces, between each cornu and the coalesced bars in the middle.

There is a squarish ear of cartilage on each side the pituitary body, growing from the trabeculæ, and looking outwards and forwards; these are the "basi-pterygoid processes" (*b.pg.*), so familiar to us in the Amniota; to these the pedicles of the suspensorium (*pd.*) are articulated. Behind these the auditory capsules are seen as very large masses, completely confluent with the chondrocranium. Below (Plate 32, fig. 2, *vb.*), the vestibule forms an almost hemispherial projection; this is caused by the sacculus, which contains the otolith (fig. 3, *ot.*).

Behind this there is a lesser eminence caused by the ampulla of the posterior canal (*p.s.c.*), between it and the larger cavity we see a shallow fossa. On the outside of this fossa the capsule projects, where it contains the horizontal canal (*h.s.c.*), and under this projection there is an oblong articular cavity for the hyomandibular.

Outside this, and between it and the superorbital band (*s.ob.c.*), there is a rounded projection. This corresponds with the lateral pre-auditory mass seen in Teleostei and ossified as the so-called post-frontal—my sphenotic ("On the Salmon's Skull," Phil. Trans., 1873, Plate 7, figs. 1–3).

Above (Plate 32, figs. 1, 5, *sp.o.*, *a.s.c.*, *h.s.c.*, *p.s.c.*), the outline of the large ear capsules is sinuous, the sinuosities being caused by the bulgings of the horizontal and posterior canals, and by the sphenotic process. Between the capsules, above, the tegmen cranii (*s.o.*, *t.cr.*) is developed both over the occipital and the post-sphenoidal regions. This roof is rather pointed behind, over the foramen magnum, and has an evenly concave margin in front; there it forms the hinder boundary of the large fontanelle (*fo.*), which is a short oval, emarginate in its narrow fore end. In front of the fontanelle there is a considerable *ethmoidal tegmen* (*t.cr.*), which covers the olfactory lobes and the small hemispheres (Plate 32, figs. 4, 5, C^{1a}., C^{1b}.); this is pointed behind in the middle, and laterally runs into the narrow arcuate superorbital band. The sides of the skull are oblique, the roof being more than thrice the width of the floor in the orbital region; these sides are mainly membranous; thus the orbito-sphenoidal cartilages are only represented by so much of the superorbital bands as belong to their territory; the alisphenoidal cartilage is merely so much of the chondrocranium as projects beyond the auditory capsule, laterally, between the basipterygoid and the sphenotic processes (*b.pg.*, *sp.o.*).

The small nasal capsules (fig. 5, *ol.*) have no separate cartilaginous roof; they are carried to the front of the snout.

The suspensorium of the mandible has retained its *primary* continuity with the ethmo-palatine cartilage, so that it is still a palato-quadrate (Plate 32, fig. 2, *p.pg.*, *pd.*); but this is quite free now from the other primary connexion, namely, that with the trabecula (*tr.*). This large arch, with its pier, foregrowth, and free mandibular bar, has undergone a similar lengthening to that of the cranium.

The pier or suspensorium is a large, oblongo-arcuate plate, ending in front in an oval sub-convex condyle, and a long, terete, pterygo-palatine process; this latter is consider-

ably longer than the main part, and reaches as far forwards as the cornu trabeculæ (Plate 32, figs. 1, 2, *p.pg.*, *c.tr.*) ; it is slightly arcuate.

The main part of the suspensorium has a thick convex lower, and a sharp concave upper, margin. The upper edge has a convex enlargement behind. This is the rounded pedicle, which articulates with the basipterygoid process of the trabecula (*pd.*, *b.pg.*). The lower margin becomes concave towards the end ; a postero-external, triangular process—the otic process—finishes the dorsal end of the suspensorium. The sub-convex, oval condyle (*q.c.*) looks forward and outward, and fits into the scooped hinder face of the articular region of the free mandible. Above its articular concavity the mandible sends forwards a large rounded ear of cartilage, convex outside (Plate 32, fig. 1, *cr.c.*) and concave within (fig. 2, *cr.c.*); this is the coronoid process of the mandible. The angular process is a free rounded spur below and behind the articular concavity. The rest of the rod (*mk.*) is terete, and almost straight; it is only slightly arched upwards and reaches nearly to the end of the snout.

The hyoid arch (Plate 32, figs. 1 and 2) has a pier which is curiously and suggestively like the suspensorium of the mandible ; but, already, it is relatively much less, being now about half as large. It has a pedicle, a free posterior process, a fore-growing rounded rod, and an articular facet for the free, inferior arch ; the only difference, here, is the absence of any *borrowed* addition at the fore end, such as the pterygoid cartilage has in the concrescent palatine.

The *pedicle* of the hyoid pier (*hm.*) is the oblong, articular head, fitting inside the oblong concavity under the auditory "tegmen;" it has no definite neck.

The free posterior process (*op.p.*) is for the opercular bone ; it is short and rounded. The fore-growing rounded rod is the "symplectic" region (*sy.*); it is terete, gently curved downwards, blunt at its fore end and enlarged near its origin; it lies anteriorly behind (under) the convex edge of the suspensorium. The body of the hyomandibular is gently bilobate and fenestrate in the middle (*hm.f.*); the articular facet for the "inter-hyal" (fig. 6, *i.hy.*) is a scooping between the two convexities of the hind margin (Plate 32, fig. 2).

The rest of the hyoid arch is not in one piece like the mandible, but in *three*, and these have, also, a large double median bar conjugating them. The first of these is a small, unciform segment of cartilage, the inter-hyal (fig. 6, *i.hy.*) ; it is articulated to the inner face of the hyomandibular by its hooked end, obliquely, and obliquely also to the top of the cerato-hyal by its base. The latter (*c.hy.*) is half the length and twice the thickness of the mandible ; it is a rounded rod, swollen near the top, and then thickened gradually to its distal end. All but the top and lower concave face is ossified.

The distal concave end is articulated to the top of a globular segment—the hypo-hyal (*h.hy.*) ; this is not ossified. The right and left segments fit into a pair of concavities on the hind face of the glossal piece, or basihyal (*b.hy.*). This is tongue-shaped, the sides are parallel, the fore end rounded ; it is moderately thick, is essentially

double, and is as long as the cerato-hyal. The subdivided, ossifying branchial arches will be described in the next stage.

The uniformity of the rapidly elongating intertrabecula is shown in the vertical section of the skull (Plate 32, fig. 4, *i.tr.*). The three trabeculæ are shown inside the lengthening snout, with its four rows of mucous glands in a second upper view (Plate 32, fig. 5); and in it, also, the position and relation of the sense-capsules and brain are displayed, and also how that the tegmen cranii (*t.cr.*) leaves the large mid brain (C^2.) unprotected.

A partial view of the chondrocranium, namely, the floor, from its upper face up to the end of the cranial cavity (Plate 32, fig. 3) shows the huge notochord (*nc.*), whose bony sheath is incomplete above, and the fore end of which is free, and but little attenuated; that part is curved but little upwards (see Plate 32, fig. 4). The fusion of the basal bands and auditory capsules is shown to be perfect, and the cupped tracts for the ampulla of the posterior canal (*p.s.c.*) and for the sacculus (*vb.*) are also seen. In front of these, on each side of the diverging parachordals—now to be called trabeculæ (*tr.*)—the basipterygoid peduncles (*b.pg.*) are shown. In the emargination behind these, in the fore part of the ear-capsules and in the occipital ring, thin films of bony matter are forming, which will become the alisphenoids, prootics, and exoccipitals; these will be shown better in the sections. The huge lanceolate pituitary fenestra (*py.*) is floored by the parasphenoid (*pa.s.*), which wedges in, in front, between the converging trabeculæ. In front of that part the chondrocranium is complete. The olfactory nerves (I.) escape from the bulbs (Plate 32, figs. 4, 5, C^{15}.) and run along to the distant nasal sacs (*ol.*) between the intertrabecula and cornua trabeculæ in the deep groove between them above. The nasal branch of the ophthalmic (5′) runs forwards outside these. Some of the bony plates are shown on the chondrocranium; the foremost of these is the first of the *maxillary chain* (figs. 1, 2, *mx′.*); and on the palato-pterygoid there are three "parastoses," namely: the palatine, pterygoid, and mesopterygoid (Plate 32, figs. 1, 2, *pa′.*, *pg.*, *ms.pg.*).

Transversely vertical sections show much that is instructive in this stage also (see Plate 33, figs. 1–13).

Section 1.—In this (Plate 33, fig. 1) the fore end of the long face is seen to be convex above and somewhat concave below. The skin is very thick and glandular; the nasal sacs (*ol.*) are simple pouches, with a thick epithelium, the tissue beneath the skin has now become osseous; in this way we get the premaxillaries, nasals, maxillaries, palatines, &c.; the plates directly over the nasal sacs are the nasals, and the palatine part of the premaxillaries is shown below the sacs. In this section we see the fore end of the prenasal cartilage or intertrabecula (*i.tr.*); it is a long oval in section, with the narrow part below and the sides compressed.

Section 2.—Here (Plate 33, fig. 2) we have the prenasal (*i.tr.*) cut through behind the nasal sacs; palatine teeth attached to bony laminæ (*pa′.*) are seen below, and similar

bony tracts (*p.ob.*) are seen, right and left above, enclosing the olfactory nerve (I.). Here the cartilage (*i.tr.*) is alate, each sharp wing being nearer the base than the top.

Section 3.—In this (Plate 33, fig. 3) the parts to be described are numerous, for the cornua trabeculæ (*c.tr.*) are cut through, and also the palato-quadrate (*p.pg.*) near its fore end. The intertrabecula (*i.tr.*) is oval in section, but it grows out, right and left, into wings, which thicken towards their outer edge and are as wide as the median bar; these are the cornua trabeculæ (*c.tr.*). Under their rounded end we see a small oval section of cartilage placed obliquely; this is the palato-quadrate (*p.pg.*). The fossa over each cornu trabeculæ is more scooped than that beneath it; in this lies the olfactory nerve (I.).

Beneath the intertrabecula, and following its curve, there is a thin lamina of bone; this is the parasphenoid; the oblique laminæ right and left of this are the vomers. The palatines (*pa'.*) are seen in the submarginal ridge, and one of the maxillary chain of bones (*mx'.*) in the lesser, outer ridge. Above, some of the superior (or ethmo-nasal, *et.n.*) and supero-lateral (or preorbital, *p.ob.*) scutes are cut through; the former protect the olfactory nerves (I.).

Part of this section (fig. 3A) is separate from the rest; it is through the lower jaw, in front of the tongue.

Here MECKEL's cartilage (*mk.*) has a short oval section; outside it we see the dentary (*d.*) as a larger and a lesser lamina.

Section 4.—This (Plate 33, fig. 4) is behind the angle of the mouth, and close in front of the cranial cavity, where the three bars (*i.tr.*, *c.tr.*) are thickest. The middle part is one-half higher than in the last section, and is broader above and below. The side bars (*c.tr.*) are twice as thick here, and are shorter, and upturned; the olfactory nerve (I.) grooves both the bars, and is more than half enclosed in cartilage. Under these thick rounded wings each palato-quadrate (*p.pg.*) is seen; it is twice as thick as in the last section, is circular, and is its own width below the trabecular cornu.

As this is close behind the gape the mandible is in two sections; the upper is small—it is the fore end of the coronoid process; at a good distance below this part the main rod (*mk.*) is severed; it is oval, with the narrow end above. Bony laminæ belonging to the preorbital series of scutes are seen supero-laterally; below the intertrabeculæ the parasphenoid (*pa.s.*) is shown; a hooked, zigzag line of bone is seen propping up the palato-quadrate cartilage; this is the pterygoid, whilst outside the mandible the dentary (*d.*) is visible.

Section 5.—This (Plate 33, fig. 5) was made through the fore part of the hemispheres (C^{1a}.) and of the tegmen cranii. The base is formed almost entirely by the trabeculæ (*tr.*) for the middle bar dies out in this region; here they are at their thickest part; they form a crescentic mass, the horns of which grow upwards and a little outwards as the lateral ethmoidal wall. These walls pass above into the convex roof; there is a superorbital enlargement where these thickish laminæ pass into each other.

The palato-quadrate cartilages (*p.pg.*) are lesser again, flattened obliquely, and are still further from the basal bars. Behind the angle of the mouth the mandible thickens rapidly; this part (*ar.c.*) shows a section oblique and sub-reniform, close in front of the articular condyle. The large mouth-cavity (*m.*) is partly filled here with a transversely oval mass—the tongue; it has a large *double* core of a soft spongy kind of cartilage; this is the exceptionally symmetrical basi-hyal (*b.hy.*).

The same kind of surface bones are cut through above; the outer film is a superorbital (*s.ob.*)—a continuation of the same chain as the preorbitals; and the inner piece is the pointed fore end of the frontal (*f.*). The pterygoids (*pg.*) are still in section, but the mandible is cut through behind its splints.

Section 6.—The next section (Plate 33, fig. 6) is through the middle of the eye-ball (*e.*), and through the hinder wide part of the hemispheres (C^{1a}.). Here the cranium is largely membranous, for the only cartilages cut through are the superorbitals (*s.ob.c.*), mere bands running superolaterally, and the trabeculæ below. The latter (*tr.*) are just distinct at this point, and are brick-shaped—a little turned up at their outer ends. Thus at this part we have the fore end of the great fontanelle (see Plate 32, fig. 1, *fo.*), and the wide orbito-sphenoidal fenestra (fig. 2, *os.f.*).

The quadrate region (*p.pg.*) is cut through here, behind the hinge of the mandible; this is still faced on the inside by the pterygoid (*pg.*), whilst another film of bone is cut through above, namely, the mesopterygoid (*ms.pg.*). Above, the frontals (*f.*) are seen in section, and below, the tongue and basi-hyal (*b.hy.*).

Section 7.—This (Plate 33, fig. 7) is post-orbital, and is through the mid brain (C^2.), and the thalamencephalon (C^1.), near the pituitary body.

The trabeculæ (*tr.*) are very small, nearly circular in section, and at their greatest distance apart. The flattened superorbital bands (*s.ob.c.*) are thrown to the side of the membrano-cranium, which is at its weakest point here. The quadrate (*q.*), which was thin above and thick below in the last, is now thick above and thin below; the long pterygoid is still on its inside, and below its out-turned thin edge a small round rod of cartilage is seen: this is the symplectic (*sy.*).

In the root of the tongue there are three cartilages cut through, the middle bar is nearly circular, the others are flattened; these are the basi-branchial and the first hypo-branchials (*b.br.*, *h.br.*). In a fold outside and below these, a thicker round rod is seen; this is the cerato-hyal (*c.hy.*). Protecting the pituitary body, the parasphenoid (*pa.s.*) has here widened out considerably; for a short space, shown in this and the next section, the roof shows scarcely any osteoblasts.

Section 8.—This section (Plate 33, fig. 8) is through the fore part of the auditory capsules and the widest part of the mid brain (C^2.), where it turns down to join the hind brain. The anterior canal (*a.s.c.*) is cut through; here the capsule (*au.*) is imperfect within, and is beginning to ossify as the prootic. The investing mass (*iv.*) is cut through where it is shooting out into the trabeculæ, and the bands are wide apart. The superorbital band has now passed into the antero-superior angle of the auditory

capsule. The pharyngeal cavity is open below, for here the great opercular fold is cut through; in it bony plates (*op.*) are forming; in its upper part the root of the symplectic (*sy.*) is severed, and below that a much larger bar with an ectosteal sheath; this is the cerato-hyal (*c.hy.*); below, the fore part of the heart (*h.*) is cut through, and above and across it the basal, distal, and cornual elements of one or two of the middle branchial arches (*b.br.*, *h.cr.*, *c.br.*). Here the parasphenoid (*pa.s.*) is of great width, undergirding not only the open basal fontanelle, but the basal plates also. The fore part of the Gasserian ganglion (5) is cut through.

Section 9.—This (Plate 33, fig. 9) is through the widest part of the hind brain (C^3.), and behind the fontanelle, for here we have the hind "tegmen" (*t.cr.*), as a thinnish layer of roof-cartilage, passing externally into the auditory capsules. At this part there is a thick band of cartilage on the inner side, in front of the large "meatus internus." Here the large ampulla of the anterior canal (*a.s.c.*) and the beginning of the horizontal canal are exposed, and outside it there is a ledge—tegmen tympani—with which the hyomandibular (*hm.*) is continuous. This is a flat cartilage; the whole of the hyoid pier is relatively small in this type.

Here the notochord is cut through, where it is enclosed by the broad, fore margin of the investing mass (*iv.*), which thins out, and curves outwards and upwards, to join the capsule. The opercular fold (*op.*) is cut through behind the lower part of the hyoid arch, which is projected forwards; the branchials (*br.*) are similar to the last, but further back in the series, and the heart (*h.*) is now cut across at its fore part.

There are several bony plates cut through in this, viz.: parietal, squamosal, opercular (*op.*).

Section 10.—Here (Plate 33, fig. 10) only the upper or main part is figured; it shows a section of the middle or widest part of the auditory capsule, where the inner wall is membranous. The anterior canal (*a.s.c.*) is cut through close to its junction with the posterior, and also the horizontal canal (*h.s.c.*) with the subdivisions of the vestibule (*vb.*). This section is behind the junction of the capsule with the investing mass (*iv.*), and shows the ganglion of the 7th and 8th nerves (VII., VIII.). The flat hyomandibular (*hm.*) is still in section, but behind its articular head; the broad parasphenoid (*pa.s.*), and the outer bony plates, are similar to those of the last section.

Section 11.—This (Plate 33, fig. 11) shows the hind part of the auditory capsule; the whole course of the posterior canal (*p.s.c.*) is seen through this back wall of cartilage. Here the capsules are some distance from the investing mass (*iv.*); above, the roof (*t.cr.*) has become deficient again, and at this part the hyomandibular (*hm.*) is cut through some distance below the condyle, and in this specimen a film of bone is seen investing the cartilage. The large notochord (*nc.*) has also a sheath of bone, and under each basal bar there is a section of the forked hinder part of the parasphenoid (*pa.s.*). One of the branchial arches (? the third) is seen in its whole extent (*p.br.*, *e.br.*, *c.br.*, *h.br.*, *b.br.*).

Section 12.—In this section (Plate 33, fig. 12) the occipital arch (*e.o.*) is cut through a

little behind its upper part, and quite behind the auditory capsules. Here the 9th and 10th nerves and their ganglia (IX., X.) are laid bare, and the heart (*h.*) is cut through at its thickest part. The investing mass has become narrow and hour-glass shaped in section; it sends upwards a cartilage which thins out gradually upwards; this is the exoccipital (*e.o.*), which becomes supraoccipital above. The exoccipital bones are forming as embracing ectostoses; the notochord has its sheath, the rudiment of the basioccipital (*b.o.*), and under the investing mass the parasphenoidal forks are seen. Here there is one pharyngo-branchial (*p.br.*) and the distal parts of two or three arches, with the basal piece (*b.br.*) lying over the heart (*h.*).

Section 13.—This last section (Plate 33, fig. 13) is close in front of the first vertebra; it catches the last pharyngo-branchial (for *h.br.* read *p.br.*), and shows some pharyngeal teeth. Only half the arch comes in here, but it shows well the outer and inner laminæ of the exoccipital bone (*e.o.*). Here the notochordal bony sheath (*nc.*, *b.o.*) is thicker, and the splintery ends of the parasphenoid narrower than in the last section.

In the last three sections bony laminæ are forming beneath the skin; these and their relations will be better understood by reference to the figures and descriptions of more advanced stages.

Fifth Stage.—Young Lepidostei *2 to $2\frac{1}{2}$ inches long.*

In this stage the skull is rapidly acquiring its permanent character (Plate 34, figs. 1, 2); the rostral part is now twice as long as the cranial cavity; in the last the pre-cranial part was not quite so long as the cranial.

This is mainly due to the growth of the intertrabecula (*i.tr.*), which already is considerably more than twice as long as the very long cornua (*c.tr.*).

The endocranium is now in this specimen (which is 2 inches long) nearly as perfect as it will be; the upper fontanelle (*fo.*) is a short ellipse, with the long diameter axial; it is relatively much less, through the growth of the tegmen cranii (*t.cr.*), fore and aft. The whole endocranium may be said to be pyriform, with an extremely long stalk; the "nose" of the *pear* is represented by the basioccipital (*b.o.*). The occipito-auditory region is semicircular above, with an apiculation over the foramen magnum; the orbital region is suddenly narrowed, and this gently lessens into the ethmoidal, which as gently becomes rostral, and the rostrum slowly lessens to its fore end, where it has two small wings. Near its root, however, it has two large wings—these are the cornua trabeculæ (*c.tr.*). The floor of the skull is still largely open (fig. 3), and the sides are occupied by the large orbital fenestræ (*os.f.*). The sheath of the notochord (*nc.*) is most completely ossified below; above (fig. 3), it is still membranous in front; the bony sheath is the basioccipital (*b.o.*); it runs a little, right and left, into the basal cartilage.

The auditory capsules are completely confluent with the chondrocranium; and their canals (*a.s.c.*, *h.s.c.*, *p.s.c.*) are to be seen through the cartilaginous wall. Above, the even form of the skull is not much altered by the canals within; below, the succulus

(fig. 2, *vb.*) largely swells the vestibular region; the form of this cavity is a short oval (figs. 2 and 3, *vb.*). The condition of the hind skull is best studied from above, in a preparation of the base (fig. 3); here the exoccipitals (*e.o.*) are seen to be forming broad borders of bone to the cartilage of the arch, and these are approaching the cephalostyle (basioccipital, *b.o.*).

Further forwards, in the angle between the capsule and the basal plate, under the Gasserian ganglion, the cartilage is being ossified as a prootic (*pr.o.*), and the wider wings which stand out from the front of the capsule are becoming the sphenotics (*sp.o.*). Also, still further forwards, the lower wings or basipterygoids (*b.pg.*) are getting a coating of bone; this ectostosis runs upwards into the side wall, in front of the capsule—it is the alisphenoid (*al.s.*).

In front of these last wings the trabeculæ (*tr.*) become bent, first outwards and then inwards, ready to join the median bar (*i.tr.*). They are rounded, solid rods. The basal fontanelle is now divided across, near its hinder end, by a narrow band, which is cartilaginous at its roots and fibrous in the middle; this is the *late* and feeble "post-pituitary wall" (*p.cl.*)—here a mere *bridge*.

The small triangular space behind is the posterior basi-cranial fontanelle (*p.b.c.f.*); the large, pinched, pyriform space in front is the pituitary space (*py.*) or anterior basi-cranial fontanelle. Its narrow anterior third runs up to the intertrabecula (*i.tr.*), which goes further back than the ethmoidal wall (*l.eth.*), and is, indeed, the rudiment of the "perpendicular ethmoid." Infero-laterally, the ethmoidal wall (Plate 34, fig. 2) is very restricted, for the orbito-sphenoidal fenestral (*os.f.*) is of great length, being extended equally in front of and behind the optic nerve (II.). But above (fig. 1, *t.cr.*) the tegmen cranii, in front, is as large as the long oval fontanella (*fo.*); behind that space the spheno-occipital tegmen is one-half longer, axially, and twice as wide across.

The three confluent trabecular bars combine to close in the fore part of the cranial cavity (Plate 34, figs. 1 and 3), only leaving an opening right and left for the long olfactory nerves (I.). When they have escaped from the skull they lie for the hinder half of their course in a deep rounded sulcus between the cornual extensions of the trabeculæ (*c.tr.*) and the huge middle bar (*i.tr.*). The three bars are at first nearly of the same width; the cornua are rounded where they first project as longitudinal wings, but they soon become narrow rods, and end in a pointed manner behind the middle of the pre-cranial region. Thence the intertrabecula is a gently compressed rod, only slowly lessening forwards, and ending as a slightly winged lobe in the end of the beak.

The first and second visceral arches (Plate 34, fig. 4) are elongated forwards like the skull, but the "pier" of the hyoid arch (*hm., sy.*) is less than half the size now of the mandibular suspensorium (*p.pg., pd.*). I have shown these with their splints attached as seen from above (Plate 34, fig. 1) and from below (fig. 2); also without the "parostoses" from their inner side (fig. 4). Their intrinsic bony centres or "ectostoses" are now clearly seen, but they are very small in proportion to the cartilage in which they

appear. The suspensorium and its free bar reach from the auditory region to a small distance behind the end of the snout; these cartilages, moreover, largely overlap each other; end to end, they would be considerably longer than the entire skull. The quadrate hinge (*q.c.*) is opposite the point where the olfactory nerves (I.) emerge, a little in front of the cranial cavity. The dorsal end of the suspensorium is bilobate; the pedicle (*pd.*) is an oblong, oblique facet, looking backwards and inwards, and articulating with a similar facet on the basipterygoid (*b.pg.*); the outer lobe is free; it is the triangular otic process (*ot.p.*); it reaches almost to the ear-capsule, but is too short to articulate with it. The main part of the suspensorium runs from these hind lobes to the quadrate hinge (*q.c.*); the inner margin is first hollow and then arched; the arch runs along the free anterior process; that edge is sharp. The outer edge is thick and ribbed on its inner face (Plate 34, figs. 2, 4); it is nearly parallel with the upper, being convex behind and concave in front. The width of this large plate is equal to half its length, and it is very elegantly sigmoid.

The quadrate hinge (*q.c.*) is a small oblong saddle, the main direction of which is forwards and a little downwards; it is convex outwardly, but has a rising inner crest (Plate 34, fig. 4), which fits closely to the articular condyle (*ar.c.*). Beyond the hinge the pterygo-palatine bar is first half as wide as its root, and then losing its inner crest, it becomes a rounded, straight, slender style, which ends very close to the point of the cornu trabeculæ (Plate 34, fig. 1, *p.pg.*, *c.tr.*).

The lower or inner face of the suspensorium is gently convex; the upper or outer face, gently concave. On the convex inner face there is a large splint-bone — the pterygoid (Plate 34, fig. 2, *pg.*); it covers more than half of the broad part of the cartilage—its antero-superior part. For some distance in front of the quadrate condyle it is continued forwards, undiminished in size; it then lessens gradually into a pointed style, which runs parallel with, and a little on the outside of, the rostrum (*i.tr.*) for three-fifths of its length.

A very narrow dentigerous bone underlies the narrow fore half of the pterygoid, and then goes beyond it up to the premaxillary, or nearly to the end of the snout. It is rather broadened in its diverging hind part, and then the right and left bones gently converge forwards; these are the *parosteal* palatines (*pa'.*).

. Along the inner edge of the suspensorium there is a narrow, thin, falcate splint, which reaches from the top of the broad part to the neck of the pedicle; this is the "mesopterygoid" (*ms.pg.*). The front of the neck of the pedicle is ossified as a small ectosteal patch; this is the "metapterygoid" (*mt.pg.*). The neck of the quadrate condyle also is ossified; this is the small quadrate ectostosis (*q.*).

From the dilated end of the intertrabecula (Plate 5, fig. 2, *i.tr.*) to the fore end of the palato-quadrate styles, there is an extremely delicate pair of bony threads; these are the vomers (*v.*). In their hinder third these bones underlie the styloid end of a bone more than twice their breadth; this is the parasphenoid (*pa.s.*); it is carinate below, widening as it approaches the basis cranii; it then narrows till it nearly reaches

the optic nerve (for I. read II.); thence it widens, loses its keel, and becomes grooved along its middle below. This bone then trebles its width, and sends out two pairs of angular projections, the lesser to support the basipterygoid processes (*b.pg.*), and the larger farther back to support the vestibular swellings of the ear-capsules (*vb.*). The bone then becomes divided into two sharp styles, which embrace the lower part of the basioccipital. The parasphenoid is three-fourths the length of the head ; it forms the only floor to the skull in the pituitary region (fig. 3, *py.*, *pa.s.*).

The bones that invest the skull above, and postero-laterally, will be described in the next stage, but partly also in the sections illustrating this. The splints of the first arch also will be described hereafter, but there is one which is figured on this Plate, namely, the preopercular. This bone (Plate 34, figs. 1, 2, *p.op.*) is a very narrow, but rather sharp splint, which is applied to, and takes the curves of, the lower edge of the suspensorium ; it is the normal splint of the mandibular suspensorium, and is more like that of a Frog than that of an osseous Fish.

The length of the free mandible (Plate 34, fig. 4), as compared with that of the palato-quadrate, is as 20 to 19 ; it is, therefore, already a very long jaw. In its hind part it is nearly as broad as its pier, and then runs to its end as a somewhat stouter rod than the pterygo-palatine above it.

The condyle (*ar.c.*) is cylindroidal, concave as seen from the side, but somewhat convex across ; there is an ectosteal "articulare" (*ar.*) in the broad part near the condyle. The angle is scarcely produced ; but in front of the condyle, above, the cartilage grows into a pedunculated crescent of cartilage, the coronoid crest (*cr.c.*) The notch between this part and the lessening rod (*mk.*) is very deep ; this leafy coronoid is convex outside and concave within. The long Meckelian rod (*mk.*) is gently arcuate and pointed at its fore end, where it nearly meets its fellow of the other side.

This skull is scarcely *amphistylic* even, much less *hyostylic*, for the pedicle of the mandibular pier is strong and well articulated, but the hyomandibular (*hm.*) is feeble, and the binding process or symplectic (*sy.*), feebler still.

The hyoid pier or hyomandibular (Plate 34, fig. 4, *hm.*), with its symplectic foregrowth (*sy.*), is about one-third the size of the palato-quadrate in front of it. The articular facet is a long, arched, convex condyle, with scarcely a perceptible neck ; behind it is the knob for the opercular ; below, this multilobate mass is sinuous, and scooped on its inner face to form the oblique condyloid facet for the interhyal. The front margin is concave, and the whole bulk suddenly lessens into a sigmoid style, bent first upwards, and then downwards, as it runs obliquely forwards to bind inside the hinder angle of the suspensorium, which is scooped to receive it. A small oval fenestra is seen in front of the middle of the hyomandibular ; and around this, below the condyle, there is an ectosteal sheath. All but the front fourth of the symplectic also is ossified as a delicate shaft-bone.

The free or postero-inferior part of the hyoid arch is more evenly massive than its pier or antero-superior part. The conjugational piece, or inter-hyal (*i.hy.*), is pyriform ;

it forms a loose joint inside the hyomandibular by its narrow upper end; and below, its inner face is scooped for the backwardly bent head of the cerato-hyal (*c.hy.*).

That segment is seven times the size of the inter-hyal joint; its head is bent back, its shoulder thickened, and has a short, separate ossification, the epi-hyal (*e.hy.*), and its shaft is rounded. The inferior condyle is hemispherical, and the main part of the thickest rod is ossified as the cerato-hyal (*c.hy.*).

The hypo-hyals (Plate 34, fig. 4, *h.hy.*) are sub-globular nodules, scooped above for the cerato-hyal, and ossified on their outside. They fit against the paired concavities of the basi-hyal (*b.hy.*)—a double, oblong, tongue-shaped, interglossal segment, as long, and twice as wide, as the cerato-hyal. This thickish plate is grooved above and below, is rounded and emarginate in front, and is composed of a spongy kind of cartilage, full of fibrous septa, which form a network in it.

There are four perfect, and one imperfect, branchial arches; they are less than half as solid as the hyoid (Plate 34, fig. 4, *br.*). In the mandibular arch, when the mouth is closed, the axes of the suspensorium and its free cartilage become coincident. In the hyoid arch they are *parallel*, not coincident; here, in the branchial arches, they are continuous, the upper being superimposed upon the lower element.

The relative size of these parts is greatly altered, and the subdivision does not exactly correspond with that of the mandibular and hyoid. The part answering to the suspensorium and hyomandibular is less than a fourth the size of that which corresponds to the mandible and cerato-hyal. Each "pier" is subdivided into two pieces—a pharyngo-branchial (*p.br.*) above, and an epi-branchial (*e.br.*) below. The upper piece is a little tongue of cartilage, turned inwards and forwards, and the lower has a short, bony shaft, and is a little rod turned directly downwards. These two segments *do not* correspond with the hyomandibular and symplectic; the upper piece has a double counterpart in the hyoid arch, namely, the hyomandibular and symplectic—one cartilage, with two bony centres in it.

Also, the counterpart of the cerato-hyal, the cerato-branchial (*c.br.*) articulates directly with its pier, the epibranchial; so that there is nothing in the branchial arches corresponding to the inter-hyal.

Instead of the hypo-branchials (*h.br.*) being short nodules, they are in the first two arches nearly as long as the cerato-branchials; are thicker than them below, but less ossified. The three joints between the four pieces seem to show no distinct joint-cavity, but are fibrous. Below, the rounded rods of the hypo-branchials fit into depression on the basal bar—basi-branchial (*b.br.*). This is, in front, a thickish, rounded rod of cartilage; it then thins out, and behind it is flat and emarginate. The first and second arch unite with the long, first basi-branchial segment; the third nearly reaches the short second piece, and the fourth is loosely attached to the side of the third piece, which is as long as the first. None of these pieces are ossified, and the first does not reach the basi-hyal, for the hypo-hyals are thrust between them.

The lessening third and fourth hypo-branchials (*h.br.*) are not ossified. The fifth

cerato-branchial (*c.br*[5].) is less than those in front of it; it is not ossified, and there is no other segment in that arch.

The branchial arches are but little modified after this; they merely increase in size, and are always small as compared with the arches in front of them. A series of sectional views will complete the illustrations of this stage.

I have now to illustrate this stage by a series of sections made from a specimen $2\frac{1}{2}$ inches long.

Section 1.—This section (Plate 33, fig. 14) is taken from near the end of the snout in front of the nasal sacs. The intertrabecula (*i.tr.*) is seen to be oval, with the larger end below. The whole snout is elliptical, with a slight convexity above, and a slight concavity below, at the mid line. The premaxillaries (*px.*) are cut through, both in their body and their palatine process (*p.px.*); they are reticulations of thin laminæ, and both above and below enclose a mucous gland.

Section 2.—The nasal sacs are cut through here (Plate 33, fig. 15, *ol.*) and the bony laminæ are more complex; the intertrabecula (*i.tr.*) has the same shape as in the last, but the whole snout is rounder above and flatter below.

Section 3.—Behind the nasal sacs other bones come into view (Plate 33, fig. 16); here the evenly elliptical rostrum (*i.tr.*) has the laminæ of the ethmo-nasal (*et.n.*) surrounding it, and on the side a mucous gland is seen in the upper half of one of the maxillary chain (*mx'.*); here the lower face of the snout is becoming convex, with a median groove; above this, right and left, vomerine teeth (*v.t.*) are seen.

Section 4.—In this section (Plate 35, fig. 1) the lower jaw also is cut through; the snout is flatter here, has a ridged lip, right and left, with sub-marginal grooves. The intertrabecula (*i.tr.*), half-way between its fore end and the cornua (Plate 34, figs. 1, 2, *c.tr.*) is circular in section, and is flanked by the layers of the thickening ethmo-nasal (*et.n.*); outside, one of the maxillary chain (*mx'.*) is seen lying over the palatine (*pa'.*), with its large tooth, and under the rostrum the two vomers (*v.*), each with a small tooth, are cut through. Below, the mandibular rods (*mk.*) are cut through at their front part, and right and left we see the solidifying substance of the dentaries (*d.*); over the cartilage towards the mid line, a small, separated style is cut through—this is the splenial (*spl.*).

Section 5.—Another section in front of the angles of the mouth (Plate 35, fig. 2) brings the tongue into view. Here the rostrum (*i.tr.*) is deep, and twice the size it had in the last section; it is flattish above, and more convex below. Here the loose reticulation of the extremely thin bony laminæ would seem to defy interpretation; but it can be classified into groups, and these groups named. Under the flat top of the beak, on each side of the rostrum, several of these thin plates are seen to be connected together, overarching a mucous gland (*m.g.*) above, and the olfactory nerve (I.) lower down. Above these is a sub-marginal groove, right and left; outside this groove the beak is convex, and from the convex part there runs inwards a thin bony flake towards

the deep, palatal chink; this is the fore part of the frontal. Below this there is one of the maxillary chain (*mx'.*) cut through, protecting a gland; and inside this, on the lateral lobe of the beak, there is a wedge-shaped tract of fine diplöe, the lower part of which carries a large tooth; this tract is the palatine (*pa'.*) cut through. In the triangular median keel of the beak there are three thin plates cut through; two of them are superficial and the third is deeper, taking the form of the rostrum somewhat, but diverging externally, and having a short crus below—this is the parasphenoid (*pa.s.*). The paired laminæ running downwards and inwards, outside it, are the vomers (*v.*) in their widest part; they are overlapped by the inner end of the frontals, externally; which, at their outer end, overlap, obliquely, the sharp end of both the cornua trabeculæ and the pterygoid cartilages (*p.pg.*). Below, the thick lower jaws have in them the section of the MECKEL'S cartilage (*mk.*), large and almost circular. There is here the flat, double tongue, with its soft basi-hyal (*b.hy.*), also double. On each side of the tongue there is a deep sulcus. The splenial bone (*spl.*), over and within the cartilage, is here at its largest size, and the dentary (*d.*) takes up a large space by its reticulations; it encloses a mucous gland below.

Section 6.—This section (Plate 35, fig. 3) is through the angle of the mouth, and thus the upper and lower tracts are continuous; the lower or mandibular region is of great height, being cut through close in front of its huge coronoid region. Here the cornua trabeculæ (*c.tr.*) are at their thickest part, or middle (Plate 34, figs. 1, 2, *c.tr.*) and are continuous by a thin oblique tract, with the rostrum (*i.tr.*) which is at the thickest part in this and the next section. Here it is semi-elliptical above, and sub-carinate below, and the thin edges of the cornua ascend to their thick outer part; the olfactory nerves (I.) lie in the hollow between the bars. A little below the cornua the pterygo-palatines (*p.pg.*) are cut through; they are oval in section, their oblique position is parallel with that of the cornua, and their size is nearly as great. The mandibles (*mk.*) are oval in section, here, and twice as thick as the pterygo-palatines; the basi-hyal (*b.hy.*) is here at its widest part. The laminæ of the ethmo-nasals (*et.n.*), and of the frontals (*f.*) run close to each other, and below the pterygo-palatine there are two tracts of reticulated bone; these are the palatines (see fig. 2, *pa'.*) below, and the pterygoid (*pg.*) above. The splenial (*spl.*) is here at its widest part, and the dentary (*d.*) is composed of a large strip of bone, externally, and of a wide network, below.

Section 7.—The position of this section (Plate 35, fig. 4) is evident, for it is through the thickest part of the coronoid process of the mandible (Plate 34, fig. 4 *cr.c.*) where this remarkable crest is separated from the main rod by a large rounded notch. Here the cornua trabeculæ (*c.tr.*) are thinning out, behind, and the intertrabecula (*i.tr.*) is most solid, it is quite round above, and sub-angulate below. The pterygo-palatines (*p.pg.*) are oval and are further from the narrowed cornua (*c.tr.*)—they are twice as near to the coronoid cartilage (*cr.c.*) Below that crest,—which is placed obliquely across the face a little tilted upwards, and the section of which is oblong, but hooked inside—the main bar (*mk.*) is a large nearly vertical ellipse; here the basi-hyal (*b.hy.*) is very

wide. The ethmo-nasals (*et.n.*) are less, and the frontals (*f.*) are larger; the palatine is gone, and the pterygoid (*pg.*) is becoming a much thicker bone. Over the coronoid process (*cr.c.*) the supra-angular bone (*s.ag.*) is seen, the dentary (*d.*) is very extensive, and is helping the supra-angulare to cover the coronoid cartilage, and growing down the outside of and coming beneath the main rod (*mk.*) The coronoid bone (under *cr.c.*) now appears inside the mandible.

Section 8.—This slice (Plate 35, fig. 5) is a little in front of the hinge of the lower jaw, and behind the outspread wings of the trabeculæ; hence, the rostrum appears to be single, although it has the trabeculæ confluent with it in its lower half. About the middle there is a slight hollow; above, it is rounded, and at its base somewhat mammillate in section; this part has the parasphenoid (*pa.s.*) fitting to it, which is thus convex instead of carinate.

The pterygo-palatine (*p.pg.*) is oblique and oval; it is nearer the rostrum than the mandible; that part (*ar.c.*) is larger than the rostrum, and is irregularly spindle-shaped in section, with its upper half slightly incurved; in its inner face the "articular" centre (*ar.*) has appeared. The basi-hyal (*b.hy.*) is now wider, and thicker; flat above, and convex behind. The ethmo-nasal bone (*et.n.*) is narrower, and the frontal (*f.*) wider; the parasphenoid (*pa.s.*) has lost its keel, and become convex and alate. The pterygoid (*pg.*) has now more diplöe above, is growing far down as a thin lamina inside the angle of the mouth; the dentary (*d.*) lies on both sides of the lower half of the cartilage; above, the supra-angulare (*s.ag.*) lies over it, and below, the angulare (*ag.*) flanks it.

Section 9.—A little further back (Plate 35, fig. 6) we get a similar section to the last, but the pterygoid (below *p.pg.*) is still more complex, above, and the articular cavity of the hinge of the lower jaw (*q.c.*, *ar.c.*) is laid open, and has a piece of the quadrate in its hinder face.

Section 10.—This is through the fore part of the eye-ball (Plate 35, fig. 7, *e.*); and here, the upper part of the chondrocranial mass is thicker; for it is in the ethmoidal region, and the olfactory nerves (I.) now run through tunnels in the closed-in skull. At this part the suspensorium is cut through in the quadrate region (*q.c.*); it appears as a sigmoid tract; thin above, thicker and rounded below, and with its upper, slightly out-turned, edge not far from the cranial axis. Below, the basi-hyal (*b.hy.*) is becoming more solid. Here each frontal is mainly a flat lamina, becoming complex externally; some of the complex outer part, however, belongs to a circumorbital. Inside the suspensorium the pterygoid (*pg.*) is a sigmoid tract of diplöe, and below the cartilage a small, triradiate tract of bone is cut through; this is the preopercular (*p.op.*).

Section 11.—Here (Plate 35, fig. 8) the cranium is cut through where the olfactory lobes (C^{1b}.) lie; it is therefore behind the proper septal portion of the intertrabecula, and shows the beginning of the tegmen cranii (*t.cr.*). The other parts are similar to those exposed in the last section, but, here, the quadrate bone (*q.c.*) is seen in the lower part of the suspensorium, as an enclosing ectosteal plate.

Section 12.—A little further back (Plate 35, fig. 9) the section is through the

hemispheres (C^{1a}.), and is behind the quadrate bone; the other parts are similar to those in the last two sections.

Section 13.—Here (Plate 35, fig. 10) the hemispheres (C^{1a}.) are wider, and with them the cranial cavity, whose walls are thinner, and laterally are partly ossified; these bones right and left, are the lateral ethmoids (*l.eth.*); they were not seen in the dissection of the lesser specimen of this stage; (2 inches long, Plate 34; the one sectioned was 2½ inches); but these bones are figured in the dissection of the next stage (Plate 38, figs. 2, 3).

Looking at the base of the cranial axis in this and the last three or four sections, we see that the parasphenoid (*pa.s.*) fits to a cartilaginous mass having a *trilobate outline* below; this arises from the fact that it was formed by the coalescence of three cartilages, viz.: the trabeculæ and the intertrabecula.

Section 14.—The hemispheres in this section (Plate 35, fig. 11, C^{1a}.) are rapidly widening, and the cranial walls are now deficient, the sides being membranous—the orbito-sphenoidal fenestra—in the lower half. The tegmen cranii (*t.cr.*) runs down the sides half way, and is grooved above; the lower edge of the cartilage just touches the optic nerve (II.). Here the base of the skull has lost its height; it is concave above, and scooped below. Here is the hinder end of the intertrabecula, and the trabeculæ (*tr.*) are each of them crested below. The suspensorium is very flat here, especially towards the top; it thickens out again above, and is surmounted there by a small extraneous bony plate—the mesopterygoid (*ms.pg.*, see also Plate 34, figs. 1, 2); here the pterygoid (*pg.*) has become a thin plate. The essentially double nature of the basi-hyal (*b.hy.*) is clearly seen in this section.

Section 15.—The hinder part of the hemispheres (Plate 35, fig. 12, C^{1a}.) are now cut through, and the tegmen cranii (*t.cr.*) is now a thin, sinuous awning thrown over the brain-cavity; it is hollow above, and convex at the sides. The frontals (*f.*) are becoming thin, and the hinder superorbitals (*s.ob.*) are thick and large. The trabeculæ (*tr.*) only are seen in this section, which is through the fore part of the long pituitary space (see Plate 34, fig. 3, *py.*); they are oval in section, and a space equal to their width is filled up between them by the parasphenoid (*pa.s.*).

The suspensorium (*q.c.*) has thickened again, and still the same bones are applied to it, namely: the mesopterygoid, pterygoid, and preopercular (*ms.pg.*, *pg.p.*, *p.op.*). Below, the section was made behind the basi-hyal, and through the first basi- and hypo-branchials (*b.br.*, *h.br'.*); outside, we see the cerato-hyal (*c.hy.*), with its bony sheath, cut through.

Section 16.—In this section (Plate 36, fig. 1) the skull is cut through close in front of the basi-pterygoids (Plate 34, figs. 1–3, *b.pg.*); in this specimen there must have been some little projection backwards from the front tegmen (*t.cr.*), not seen in the one dissected; this would have made the fontanelle heart-shaped, instead of circular.*

* This projection from the front "tegmen" was seen in the last stage (Plate 32, fig. 4, *t.cr.*), where the fontanelle has a similar shape to that of a young Salmon of the 2nd week. ("Salmon's Skull," Plate 4, figs. 1, 2.)

Here the cavity of the skull is at its widest part; further back the width of the head is due to the addition of the auditory capsules, but the hind brain (C^3.) is only half as wide as the mid brain (C^2.). Here the razor passed from the front of the fontanelle, above, to the middle of the fontanelle, below, just where the trabeculæ pass into the investing mass (*iv.*), and behind the optic foramina (see Plate 35, figs. 11, 12); the section is therefore somewhat oblique, backwards and downwards. The slight projection from the front tegmen (*t.cr.*) is wide apart from the alisphenoidal region, or lateral band of cartilage (*al.s.*), which is thickish, convexo-concave, and occupies more than half of the side wall.

Below, under the thalamencephalon, the parasphenoid (*pa.s.*) is thick and narrow, and is strongly wedged in between the narrowest part of the basal bars (see also Plate 34, fig. 3, *tr.*, *iv.*, *pa.s.*), which are oval in section, and slightly tilted outside. Between them and the alisphenoidal tract (*al.s.*), part of the trigeminal nerve (V.) is seen. Above, the parietals (*p.*) are cut through, and also a lateral bone—the squamosal (*sq.*). Here the suspensorium (*q.*) is, in section, like a drumstick, but feeble below and out-turned, for it thins down towards its lower thickening, and there bends outwards over the small, round symplectic (*sy.*). Above, it is round, very solid, and sheathed at the very top with a bony tract; this is the "metapterygoid" (*mt.pg.*) which is cut through.

Below, the preopercular (*p.op.*) is seen as a small tract of diplöe, enclosing a mucous gland; inside it, the cerato-hyal, with its ectostosis (*c.hy.*), is severed, and further inwards the basi-branchial and the first and second hypo-branchials (*b.br.*, $h.br^1$., $h.br^2$.).

Section 17.—We have now a section (Plate 36, fig. 2) close in front of the pituitary body, but missing it; it is through the infundibulum (*inf.*) below, and the mid brain (C^2.) above, and catches the terminal point of the small tegminal projection; this thin slice was the next to the last, which is not always the case in those which are figured.

Here the basipterygoid processes (for *q.* read *b.pg.*) are seen as thick wings growing from the front part of the investing mass;* they are partly ossified by the lower edge of the alisphenoidal centre; they are thin at their root, thick outside, and they dip a little; above them, the 5th nerve (V.) is cut through. Here the parasphenoid (*pa.s.*) sends out its first pair of angular projections (Plate 34, fig. 2), so that it forms a bony floor to the skull. Above, the parietals and squamosals (*p.*, *sq.*) are seen in section, and also one of the numerous post-orbital scales. The symplectic (*sy.*) is cut off where it has a bony sheath, as it passes forwards to the suspensorium. The cerato-hyal (*c.hy.*) is trilobate here in section; outside, it is the interopercular (*i.op.*); the branchial sections are of the same bars as in the last.

Section 18.—This (Plate 36, fig. 3) is through the fore part of the hind tegmen (*t.cr.*), and where the mid brain passes into the hind brain (C^3.). Here the head is slightly concave above; the roof-cartilage is rather thin, and forms part of a nearly complete cincture, for it is confluent here with the fore part of the auditory capsule (*au.*), which in

* Two errors escaped me in the lettering of this figure,—for *q.* read *b.pg.*, and for *mt.pg.* read *iv.*

turn passes into the investing mass (*iv.*) below. There the cartilage is a thick wedge, right and left, and the space between the two wedges is filled in by the parasphenoid (*pa.s.*); in front of the apex of the notochord. Where these basal plates pass into the capsules there the facial nerve (VII.) is severed, and further outwards the capsule has a groove under it in which the fore part of the head of the hyomandibular (*hm.*) is seen; it is partly ossified above and also below as the symplectic. A neat lip, the rudimentary "tegmen tympani," is seen outside the rod, and above it the ampulla of the anterior canal (*a.s.c.*), whose arch also is severed higher up. The bony tracts below are parts of the large, infolded, angular interopercular (*i.op.*, see also Plate 37, fig. 4, *i.op.*).

The second, third, and fourth hypo-branchials and the middle of the basi-branchial ($h.br^{2-4}$., *b.br.*) are severed, and the gills are seen depending over the fore part of the heart (*h.*).

Section 19.—The roof is now in the superoccipital region (Plate 36, fig. 4, *t.cr.*); it is twice as thick and only two-thirds the width at this part, as compared with the last. Here the hind brain (C^3.) has only membranous sheets interposed between it and the auditory labyrinth, which is deficient in its cartilaginous wall in this, the region of the "meatus internus," where the auditory nerves (VIII.) enter. The section of the hyomandibular (*hm.*) is here behind the symplectic; above its head the horizontal canal (*h.s.c.*) is cut through and the end of the arch of the anterior canal (*a.s.c.*) is seen to come close to the great inner "fenestra" of the capsule. Here, as in Sharks and Skates, the basal plate (*iv.*) projects beyond the capsules, and in the angular space the 7th nerve (VII.) is cut through.

Below, this section is still in front of the notochord, but the parachordals (*iv.*) bend down very near to each other; they are supported by the parasphenoid (*pa.s.*). Here the branchial arches (*h.br.*, *b.br.*) are cut through near their hinder part; below, their gills (*g.p.*) are seen hanging over the heart (*h.*), and the interopercular is seen outside the hyomandibular (*hm.*).

Section 20.—In this slice (Plate 36, fig. 5) the apex of the notochord (*nc.*) is cut through, and here the auditory capsules have recovered their inner wall; the end of the horizontal (*h.s.c.*) and the part leading to the common sinus of the anterior (*a.s.c.*) and posterior canals are cut across. The vestibule (*vb.*) is lessening here, where the back of the "sacculus" is shown. The hyomandibular is severed behind its head, and outside it the interopercular and subopercular are shown in section in the fold (*op.*). Here a ganglionic mass belonging to the 9th and 10th nerves (X.) is brought into view; and above, the parietals and one of the temporal series (*s.t.*) are severed.

Section 21.—The back of the auditory capsule, with the ampulla and hind part of the posterior canal (Plate 36, fig. 6, *p.s.c.*), are now severed; here the double passage for the 9th and 10th nerves and the nerves themselves (IX., X.) are seen; the bony laminæ are severed that are finding their way into the back of the auditory capsule; in the cavity of the ampulla, and from the foramen over the top of the oblique lower

part of the occipital arch, there are parts of the spreading exoccipitals (*e.o.*). The opisthotic and epiotic are formed over the posterior canal *later* (see Plate 38).

The two halves of the investing mass, below, form a rest for the oblique plates of the upper part or arch, and are only slightly tilted upwards outside; they are thick inside and flattish on the outside, and have the notochord (*nc.*) between them; this rod is, here, ensheathed in bone, and this thick bony sheath has sent a wing, right and left, over the basal part of the moieties of the investing mass, which are curling over their external edge, as far as to the edges of the underlying parasphenoid (*pa.s.*); this ectosteal growth is the basioccipital (*b.o.*). The top of two of the branchial arches (*p.br.*), the parietal (at its end), and a supra-temporal bone are also seen. In this section the occipital arch is seen to be two-winged, right and left; in the last stage (Plate 33, figs. 12, 13, *iv.*) the section, here, was like an hour-glass.

Section 22.—The roof is now (Plate 36, fig. 7, *s.o.*) very thick, and here the vagus nerve only (X.) is seen with its ganglion; the back wall of the auditory capsules nearly meet above; the basal plate (*iv.*), between the halves of which the osseous sheath of the notochord (*nc.*) is seen, with its right and left basioccipital wings (*b.o.*), is surmounted by the side plates of the arch (*e.o.*). Behind the horizontal canal the combined occipital arch and auditory capsules form large thick shoulders of cartilage; whilst, above, the arch has three roundish crests (*s.o.*). Here the basal plate (*iv.*) is thicker, and as in the last, the parasphenoid is corrugated; the wings of the basioccipital bone (*b.o.*) do not yet invest the lower face of the cartilage; the opercular (*op.*), and a post-temporal scute, are seen in section, as also some parts of the hinder branchial arches (*br.*), with their pectinate gills and grooving vessels. Here the peculiar *four-fold* nature of the occipital arch is well seen, the oblique sides resting on a projecting threshold, through which the notochord, with its bony sheath, runs.

Section 23.—The last of the sections (Plate 36, figs. 8, 9) figured is through the thinner hind edge of the occipital ring, which is lozenge-shaped, and somewhat winged, right and left, for the side-walls have the same obliquity as the halves of the archway above; here the threshold is not so wide as in the last section; it is narrowing towards the end of the projecting basioccipital (see Plate 34, figs. 1–3, *b.o.*).

The exoccipital ectosteal plate (*e.o.*) is seen inside the converging arch, the right and left plates nearly meet above, and there is no key-stone piece or supraoccipital bone in the rounded median part. Here the notochord (*nc.*) lies impacted between the basal plates and their ascending arch; it is the core of a strong basioccipital bone (*b.o.*), which strongly encloses it, the soft tissue spreading in radiating lobes in the thickening bone-substance. Laterally, the bone has spread so as to enclose the halves of the investing mass, and runs beyond these parts; it grows as a right and left sharp plate. Here the wide corrugated parasphenoid (*pa.s.*) is in two parts, for it is forked behind (see also Plate 34, fig. 2, *pa.s.*).

Sixth Stage.—Young Lepidosteus, 4 *inches* 5 *lines long.*

In this stage the dermal scutes are so well developed that they can be named and classified ; I shall describe them first, and the endocranium afterwards.

Notwithstanding the size of this specimen it had still the remains of the embryonic suctorial disk at the end of the snout (Plate 37, figs. 1–3), forming a pad on the end of the premaxillaries (*px.*), and lying in a horizontal plane. The lower jaw just reaches this part, the disk, itself, overlapping it.

The rostral region of the head is twice as long as the cranial ; the opercular bones (*op.*, *s.op.*), pass behind the projecting basioccipital (*b.o.*)

The mandibles are two-thirds the length of the head, and as in embryo Frogs, are articulated to the quadrate *in front of the eye-ball* (*e.*) ; in old Frogs the condyle of the quadrate may reach as far backwards as the opercular folds do in this Fish.

The bony scutes of the hinder part of the head and face do not differ much from those covering the body, except in size ; but in the rostral region, both above and below, but especially below, many of the bony plates are styles of great length and tenuity ; this is a specialization quite like that which is seen in the skulls of longirostral Birds, and in some extinct Sauropsida, *e.g.*, the *Ichthyosaurus.*

Most of the bones of the roof are not difficult to decipher, for the eye detects quickly the parietals, frontals, and squamosals (Plate 37, fig. 1, *p.*, *f.*, *sq.*) ; but nearly the whole extent of the rostrum has to be traversed before we reach the true nasals. These bones (*n.*) are small crescentic scutes that cover the small, distal olfactory capsules (*ol.*) But along the top of the rostrum, from the ethmoidal region, where the frontals diverge nearly to the nasal roofs, two long, narrow styles of bone are seen ; these I propose to call "ethmo-nasals" (*et.n.*) ; they are manifestly separate centres that correspond to the elongated hinder part of the nasals of a Bird.

The olfactory sac, in both Ganoids and Teleosteans, is devoid of a proper paraneural roof, and the bone covering it is merely one of the many "slime-bones" seen in the skulls of these Fishes ; still, that scute which directly covers the olfactory organ has the first claim to be called the nasal. The frontals (*f.*) in their foremost third are divarcated and styloid, embracing the hind end of the ethmo-nasals (*et.n.*) ; they are wide where they meet over the antorbital region, become pinched up to their hinder fourth, and then widen most where they are overlapped by the parietals. These latter bones (fig. 2, *p.*) are large and oblong, covering the skull well from the middle of the eye-balls to the back of the ear capsule ; they are flanked and overlapped by the temporal series.

The principal temporal bone is the squamosal (*sq.*) ; it is a long and irregular triangle, with its sharp end foremost ; its broad end is overlapped by the second large temporal (*s.t.*), which covers the hinder part of the parietal as a rounded scale. Under it there is a lesser pair, and under these upper, larger bones, there is a considerable patch of small scutes margined by the circumorbital series in front, and the angulated interopercular

(*i.op.*), behind. The circumorbital series is a very perfect ring of small scutes round the eye-socket; of these the antero-superior scales are the largest. A short chain of three or four small scutes runs forwards from the *superorbital* part of the ring; these may be called *preorbitals* (*p.ob.*); they are tilted up and form a sort of "eave" to the large convex coronoid part of the mandible. There, indeed, in front of the eye-balls, the skull is pinched inwards, and set, as in a vice, between the high hinder part of the lower jaw, whose steep, almost vertical, hind margin chafes, so to speak, right and left, against each circumorbital ring (Plate 37, fig. 1).

Below the tilted preorbitals there is another short, feeble chain of three or four scutes; the last but one of these (*m.x''.*) is as long as the others together, and has all the relations of the free part of the edentulous "os mystacum," or maxillary of typical Teleosteans; the little scute behind it (*j.*) shows the same relations as the small malar (jugal) of many Teleostei.

Outside of and protecting the sub-marginal row of mucous glands, there is a long chain of bones (see Plate 32, fig. 5, *m.c.g.*, and Plate 37, figs. 1, 2, *m.x'.*); this series of scutes is the continuation of the *mystaceum* series (*m.x''.*, *j.*) but thrice their width; this may be called the *maxillary chain*. This is composed of about fourteen or fifteen very similar scutes; they are oblong, their width being about half their length. In front of these the small premaxillaries (*px.*) are seen to be distinct, right and left. Each moiety (or centre) is pointed in front, has a small palatine plate and a dentary edge with sharp teeth; these rows of teeth (fig. 3, *px.*) meet in front at an acute angle.*

Behind the palatine plate of the premaxillaries, right and left, there is a long bone in close contact with its fellow of the opposite side, and so slender that the two together are not so wide as a single ethmo-nasal (fig. 2, *et.n.*); these "needles" are the vomers (fig. 3, *v.*); they become covered with a very fine rasp of teeth, and are nearly half the length of the entire skull.

Bounding these, along the palatal face of the rostrum, there is a pair of bones one seventh longer than the vomers, and twice as wide; these are the "parosteal palatines" (*pa'.*). These bones become invested with a rasp of teeth a degree coarser than that on the vomers.

In the long valley between these palatine splints and the maxillary chain there is a row of *large* sharp teeth, and on the edge of the chain an outermost row of *small* sharp teeth. A very long carinate, trough-like bone runs over the hind part of the two vomers for a considerable distance, and then extends to the end of the skull; on escaping from them it appears also rough, with a fine rasp of teeth. Further back these teeth cease, but the bone is carinate up to the basi-pterygoid (*b.pg.*); this is the parasphenoid (Plate 37, fig. 3, *pa.s.*) This bone is wider in the ethmoidal than

* In an old specimen I find a flat sub-arcuate scute binding across in front of the distant premaxillaries; this latter bone might be thought to be an edentulous azygous premaxillary and the two next behind it, not premaxillaries, but the foremost of the maxillary chain; I incline to call it a prenasal.

in the post-orbital region, but it then widens to thrice its breadth even in the ethmoidal region. It flanks the basipterygoids (*b.pg.*) with a pair of small wings, is spread out under the auditory capsules (*au.*), and applies itself as a forked splint to the under face of the basioccipital (*b.o.*). Behind, for three-fifths of their length, the palatine splints (*pa'.*) are bound on their inner edge by a larger, but similar bone; this is the pterygoid (fig. 3, *pg.*); both these bones are seen in their relation to the suspensorium in other figures (Plate 37, fig. 4, and Plate 38, fig. 5, *pa'.*, *pg.*). The pterygoids acquire a fine bony rasp when they lie close to the palatal surface. Each bone is a long style in front, and then widens gradually so as to become a broad spatula in the orbital region.

The styloid palato-pterygoid cartilage is applied to its outer face above, but the bone passes backwards, and invests three-fourths of the inner face of the broad suspensorium (see Plate 38, *pg.*), ending behind, with a thin, rounded margin.

When these parts are removed from the rest of the skull (Plate 37, fig. 4, and Plate 38, fig. 5) their parosteal relation to the prognathous suspensorium is clearly seen.

Over the edge of the suspensorium, in its broadest part, there is a *third* parostosis; this is the mesopterygoid (Plate 37, fig. 4, and Plate 38, fig. 5, *ms.pg.*). It is a thin, falcate bone above, one-sixth the length, and one-sixth the width, of the pterygoid.

A *fourth* splint is applied to the suspensorium, and this, like the last, is extremely small as compared with what is seen in the Teleostei; this is the preoperculum (*p.op.*); this bone is falcate, narrow, gently curved downwards, pointed behind, where it lies on the interopercular, and roughly notched in front, where it binds on the outside of the quadrate bone (*q.*); it is only one-third the length and one-third the width of the succeeding bone—the interopercular (*i.op.*); whereas in the Teleostei it is much the larger bone, as a rule.

The free part of the lower jaw, or mandible, is of great length, and the dentary bone covers it from end to end (Plate 37, fig. 4, *d.*); on the inside (Plate 38, fig. 5, *d.*) it is only seen at the edges of the jaw. Under its upper edge, on the inside, a much smaller bone, three-fourths its length, binds on the upper edge of the cartilaginous axis (*mk.*); this is the splenial (*spl.*).

Behind the splenial, on the inner side (Plate 38, fig. 5 *cr.*) the coronoid is seen as a pedate tract of bone with its heel behind; it binds on the inside of the fore part of the large cartilaginous coronoid (*cr.c.*). Under the short angular process of the articular cartilage there is a small angulare (*ag.*), and outside the large, ear-shaped coronoid cartilage, on its convex face, there is a considerable scale of an oval shape, and placed obliquely forwards and upwards; this is the supra-angulare (Plate 37, fig. 4, *s.ag.*).

The specialised "scutes" just described belong to the mandibular arch; those next to be noticed belong to the hyoid. On the knob of the hyomandibular a large oval scute is articulated by its capped fore end: this is the operculare (Plate 37, fig. 1, *op.*); below this a similar bone is seen, but of an uncinate or semi-crescentic form, with its sharp end behind, and its upper edge inside the operculare; this is the sub-operculare (*s.op.*).

Binding on the fore edge of the two last, we see an angulated sub-crescentic bone, with its concave edge above, its angulated margin below, and its front point binding under the hind point of the preoperculare. This is the interoperculare (Plate 37, fig. 4, and Plate 38, fig. 5, *i.op.*). These three bones are the hyomandibular splints; those now to be described belong to the cerato-hyal; these are the branchiostegals: they are beneath and within the great operculum (Plate 37, fig. 1, *br.s.*), and are attached in front to the cerato-hyal. Generally *seven* in number in the Teleostei, there are only *three* here, as in the Carp. These bones are narrow and falcate, with their concave margin above; the uppermost is the largest; the lower is the least.

The remainder of the bones which I have to treat of are *intrinsic* centres, or "ectostoses;" they will come under notice, now, in a description of the endocranium, most of which, however, is cartilaginous.

The endocranium at this stage differs but little from that of the adult, in which, although the bony centres become dense and relatively larger, are yet not altered, either in their number or relations, to any appreciable degree.

In this skull, the "prenasal rostrum," or intertrabecula, is as much developed as in the most specialised of the Selachians—namely, the "Pristidæ," or *Saw-fishes*—much more than in the ordinary Skate ("Raiidæ"). Here the length of this precranial region is, as compared with the cranial cavity, as 14 to 5, or nearly three times as long. In an old specimen the cranial cavity is only 2 inches long, and the whole skull $12\frac{1}{2}$ inches, or 2 to $10\frac{1}{2}$; the brain has, relatively, retreated. Measured from the quadrate condyle, in this young stage, we get the same proportion as the measurement of the precranial to the cranial; in the old the prequadrate region is 9 inches long, and the post-quadrate $3\frac{1}{2}$ inches.

This remarkable pyriform, long-stalked skull owes its greatest expansion to the superaddition behind of the large ovoidal auditory capsules, and next to them to the greater size, in the young, of the mid brain; it soon narrows in over the small hemispheres. As in the last stage, the roof of the mid brain is membranous—this is the large circular fontanelle (Plate 38, fig. 1, *fo.*), the margins of which are very moderate bands of cartilage—the postorbital part of the superorbital bands (see Plate 30, fig. 8, *so.b.*).

Below (Plate 38, fig. 3, *py.*, *pa.s.*) there is a rather large and lanceolate pituitary fontanelle; and inside the orbits (Plate 38, fig. 2, *o.s.f.*) there are the long "orbito-sphenoidal fenestræ." The upper fontanelle (*fo.*) takes up about a third of the roof, but it is not so long as either the fore or the hind part of the tegmen cranii (*t.cr.*). Thus although this is rather a well-developed chondrocranium it has four large membranous deficiencies in it.

The basioccipital (Plate 38, figs. 1–3, *bo.*) might be taken for the centrum of the first vertebra—it projects so far behind the exoccipitals (*e.o.*). The bony matter, which did occupy much of the sheath of the cranial notochord, is now mainly confined to its hind part, and forms a four-sided mass; this mass does not run forwards into the rest of the notochord—at least on its upper surface (Plate 9, fig. 3, *nc.*).

This rugous bone is broadest behind, where it is scooped for the first vertebra; above, it is flattened; its fore end is emarginate, and its two oblique antero-lateral faces are joined by suture to the exoccipitals (*e.o.*)

These bones are small lunate tracts behind the passages for the 9th and 10th nerves (IX., X.); the rest of the occipital arch is devoid of bone, for the superoccipital is absent, as in the Amphibia; that region projects, as an obtuse angle of cartilage, over the foramen magnum.

The auditory capsules project well into the basal plate (*iv.*); their canals (*a.s.c.*, *h.s.c.*, *p.s.c.*) are large, and easily seen through the transparent cartilage; both above and below they send their diverticula inwards towards the mid line, so as to make the roof and floor of the skull into the shape of an hour-glass. The upper part spreads outwards over the horizontal canal, covering the facet for the hyomandibular (*hm.c.*); further inwards, below, the swelling "sacculus" on each side makes a notable bulging, which is partly floored by the parasphenoid (*pa.s.*). Postero-laterally, the capsules are but slightly angulated; but in front they grow outwards and forwards into an ear-shaped projection, which is separated by a round notch from the root of the super-orbital band (*s.ob.c.*). That process is the "sphenotic" outgrowth of the chondrocranium in front of the capsule; it is becoming bony (Plate 38, figs. 1, 2, *sp.o.*); also below, in front of the capsule, and surrounding the chinks and openings for the 5th and 7th nerves (V., VII.), the prootic centre (*pr.o.*) is spreading into the cartilage; in front it runs into the back of the corresponding basipterygoid (Plate 38, fig. 3, *b.pg.*); and behind it has reached the concavity for the sacculus (*vb.*)

Also above (figs. 1 and 4), an irregular bony tract is seen imperfectly divided into two patches, which lie over the ampulla of the posterior and the end of the horizontal canal (*p.s.c.*, *h.s.c.*). The upper part is the rudiment of the epiotic (*ep.*), the lower portion of the opisthotic (*op.*).

In front of the basipterygoid (figs. 2, 3, *b.pg.*), and rising upwards from it into the limited tract of cartilaginous wall between the orbito-sphenoidal fenestra and the ear-capsule, there is a bony tract, smaller than the prootic and next in front of it; this is the alisphenoid (*al.s.*).

Along the skull base, in front of the projecting basioccipital, there is no intrinsic bony centre, and laterally, the whole orbito-sphenoidal region is membranous.

But where the skull is closing in, in front, the rapidly narrowing cranium has a short tract of cartilage in its sides; this is the lateral ethmoidal region; the free border of this cartilage in front of the fenestra is ossified as a crescentic patch (Plate 38, figs. 2, 3, *o.s.f.*, *l.eth.*); this answers to the so-called prefrontal of the Teleostei, but it does not grow out into ethmoidal wings, as in those types.

A very important change has taken place inside the basis cranii, for now there is a very definite "posterior clinoid" *bridge*, not *wall*, of cartilage (Plate 38, fig. 3, *p.cl.*); it is small, very narrow in the middle, and runs straight across, joining the roots of the trabeculæ (*tr.*) together, but lying only at a small height above them.

This is a very feeble rudiment of the thick and high wall, which is developed in this part in most of the "Amniota," where it runs up in the deep fissure under the mid brain. However, even here it divides the basi-cranial fontanelle into two parts, a large anterior (*py.*) and a small posterior space (*p.b.c.f.*).

Thus it is evident that in this, as in other kinds of Ichthyopsida, the basis-cranii is much less affected by the mesocephalic flexure than it is in the Sauropsida and Mammalia.

The main pituitary space (Plate 38, fig. 3, *py.*) is lessened by the ingrowth of the trabeculæ (*tr.*); but in front, it is filled in by the hind part of the long intertrabecula. The trabeculæ are bowed out right and left, between the 5th and 2nd nerves (V., II.); the 1st nerve (I.) escapes from the front of the enclosed end of the cranium, and runs all the distance to the nasal sacs close to the sides of the intertrabecula (*i.tr.*)

The paired trabeculæ (*tr.*) do not end where the skull has closed in; in front of the narrowed tegmen cranii (Plate 38, figs. 1, 2, *t.cr.*) the intertrabecula is seen to be narrow above, and to have narrow wings running along its sides.

These wings soon dilate, so as to give the rostral part of the skull an oval widening along the front *two-fifths* of its *hinder fifth.* These parts are the cornua trabeculæ, and although they are so short now, they were (Plate 30), once, the main part of the skull in front, and for some time came little short of the end of the snout. Now, they are like the right and left sides of a lanceolate leaf, with a huge mid-rib; only their terminal point is free, and the 1st nerve runs in a groove between them and the long rostrum.

The rostrum (*i.tr.*) is very uniform up to near the front end; it then becomes slightly alate before ending in a blunt and somewhat decurved point (*p.n.*); its section is nearly oval, the thicker end below.

The suspensorium (Plate 37, fig. 4, and Plate 38, fig. 5) retains the form it had in the last stage (Plate 34), but it is twice as large, and its bony centres are now perfect. The upper bone is the metapterygoid (*mt.pg.*), it occupies the neck of the suspensorium, leaving cartilage, however, on the concave articular facet—for the basipterygoid—and also on the short round "trochanter," below the joint; this spur is the arrested otic process (*ot.p.*).*

The quadrate (*q.*) is a bony quadrant running, at its angle, close to the articular condyle (*q.c.*); this latter is an elegant convexo-concave trochlea, with its largest convexity on the outside. The main part of the body of the suspensorium is unossified; it is a large oblong tract, with its postero-inferior angle rounded off; it is rather hollow outside and convex within, where it is invested by the pterygoid bone (*pg.*).

The pterygo-palatine rod (*p.pg.*) is unaltered since the last stage; it never ossifies, and reaches as far forwards as the cornua trabeculæ (*c.tr.*).

The articulo-Meckelian rod (*mk.*, *ar.*) has increased in size (both actually and

* In Plate 38, fig. 5, below, for *pa.* read *pl.*

relatively) ; its intrinsic centre also, the articulare, has become two separate points of bone (Plate 38, fig. 5, *ar.*). The rest of this long, subarcuate, terete rod (*mk.*), runs along the grooved inner face of the dentary (*d.*) nearly to its distal end. The coronoid crest (*cr.c.*) is a very large "ear" of cartilage ; it is convex outside and hollow within ; its fore part is a free lobe.

The hyomandibular (Plate 37, fig. 4, and Plate 38, fig. 5, *hm.*) is a remarkable bar, about half the size of its "serial homologue"—the suspensorium. Its arched, extended head is a convexo-concave condyle for articulation under the horizontal canal; behind this there is a cartilaginous knob for the opercular bone. The bony shaft is short, pinched in the middle, and has an oval fenestra near its front third. Below the shaft it swells out into a solid bilobate mass, the lesser lobe being behind. In front of the fore lobe, on the inside, there is a concavity for the inter-hyal (*i.hy.*). The bar from that point becomes the small sigmoid symplectic (*sy.*) ; it is bent downwards suddenly, and then runs straight forwards to lie along the inside of the hinder third of the lower edge of the suspensorium.

Its bony shaft occupies its hinder two-thirds ; where it becomes straight, there it has a small bony elbow; its fore end is a blunt point (Plate 38, fig. 5, *sy.*).

The inter-hyal (*i.hy.*) is a small pyriform cartilage, its narrow end fits into the concavity in the hyomandibular, and its broad end has a cup on its inner side for the head of the cerato-hyal (*c.hy.*).

The latter segment has a "trochanter" behind its small rounded head ; its shoulder is ossified as a separate epi-hyal (*e.hy.*) ; the main shaft (*c.hy.*) has its own centre ; it is narrower in the middle, and is only separated from the stylo-hyal by a tract of cartilage.

The rounded lower end of the cerato-hyal fits into the oblique shallow cup of the sub-globular hypo-hyal (*h.hy.*) ; this short segment is ossified on its outer face ; at present, at any rate it has no second centre, as in the Teleostei ; but in these, as in *Acipenser*, it is completely segmented off from the cerato-hyal.

The basal piece (*b.hy.*) is a large "inter-glossal" plate as long as all these three segments above it ; it is oblong, rather pinched in the middle, emarginate in front, thickish, and somewhat fibro-cartilaginous, having cross-bands and reticulating, connective fibres, wrought into it on its upper surface, and its hyaline cartilage somewhat softer than in the other parts.

The basal piece of the branchial system, and part of the first part of hypobranchials (*b.br.*, *h.br'.*) are figured. For the rest, I must refer to the figures and descriptions of the last stage ; these parts have not altered in any important degree —except in size.

Comparison with other types, and Summary.

As soon as the primordial cranium becomes sufficiently differentiated—as hyaline cartilage—to be distinguished from the rest of the cephalic mesoblast, we find a

peculiarly simple foundation for all the aftergrowths. In Stage 1, in embryos $10\frac{1}{2}$ m.m. long, nearly all the parts of the chondrocranium—including in this term the visceral arches—are present; the hinder arches become broken up, afterwards, but the two first, and largest, the mandible and hyoid, are already as much segmented as they will be in the adult.

The skull-floor, only, is developed, as yet, and the rostral part, in front, is not chondrified, but its outlines can be traced, and the roof and walls of the skull are merely developments from the basal bands.

Those bands in this type lend no support to the theory of the visceral (or ventral) nature of the *pro*-chordal tracts or *trabeculæ;* they are, manifestly, mere continuations of the undivided *para*-chordal cartilages, which expand and contract in relation to the parts around and over them. They diverge from the front third of the notochord, as though their relation to it was not intimate, and show—for a long while at least—no tendency to grow up, with that axis, into the hollow of the mid brain.

I see nothing in this lyriform basal skeleton of the skull but an undivided *basi-neural* structure comparable to, and a *primary cephalic variation* of, the tracts that form the paired rudiments of the *neuro-central* cartilages of the spine. The cessation at the end of the notochord (mesially), and close behind the oral opening, laterally, of the hypo-blastic layer, causes all the pre-oral and pre-pituitary parts to be, in a sense, imperfect; they are developed as porches and outworks to the full and complete structure further back, but this does not destroy their homology, nor break their continuity with the parts formed from their own embryonic layer, of which they are the direct ongrowths.

Yet all parts growing out,—forwards, upwards, or downwards,—in front of the perfect axis, which ends close in front of the infundibulum, must be very cautiously named as "serial homologues" of the perfect base and its upper and lower arched growths; they are probably mere *outgrowths;* at most they are only *rudiments.*

The *primary* trabeculæ are merely direct *on*-growths of the parachordals; the cornua trabeculæ are *out*-growths of the trabeculæ.

The intermediate element, or intertrabecula, is a fresh outbreak, so to speak, of the median mesoblast of the axis, which is tubular, behind, where it encloses the notochord, but, re-appearing in front, beyond it, it shoots forth as a *solid process* of the skeletal axis.

Close to the fore end of the primary trabeculæ there arises a similar but rather smaller bar, and the two parts are so close together that they chondrify continuously; these side bars are the palatine cartilages, evidently rudimentary structures.

Here they are not distinct from the long spur (pterygoid cartilage), which shoots forwards from the dorsal element (suspensorium) of the mandibular arch; this is like what we see in the Tadpole, but unlike that which is found in Skates, Teleosteans, and Urodeles. Thus, with the palatine included, the suspensorium here is a *palato-quadrate;* in the Skate, Teleostean, and Urodele the suspensorium is a *pterygo-*

quadrate. As in the Tadpole, the fore end of this bar is fixed; as in the Teleostean Urodele, and adult Frog, the hind part, or pedicle, is free.

As in the Tadpole, the suspensorium is sub-parallel with the axis of the skull, and the free mandible (MECKEL'S cartilage) grows forwards and inwards; that condition is temporary in the Batrachian, it is permanent in *Lepidosteus*.

As to the development of the basal bands of the skull, this type agrees with the Selachians and Teleosteans (*Salmo*) in the synchronism of the *para-* and *pro-*chordal tracts; but in Batrachians, Urodeles, and Marsipobranchs, the *trabeculæ are developed first;* they embrace the fore end of the notochord closely, and are both *para-* and *pro-*chordal; afterwards the hinder parachordal region is chondrified, separately in Urodeles, and continuously in Batrachians and Marsipobranchs.

The development of the complex hyoid arch is very different in this *Holostean* Ganoid, and in the *Chondrostean* Sturgeon, from what we find in Teleosteans, Batrachians, and Urodeles.

In the Salmon the primary bar breaks up into two long bands, with a short segment below; the foremost is the larger, retains its connexion with the ear-capsule, widens above as the hyomandibular, and narrows, antero-inferiorly, as the symplectic region.

The narrower, hind band becomes postero-inferior in position, keeps the small distal segment, and acquires a new, small segment, above, by which it becomes attached to the space between the hyomandibular and symplectic; the *late*, small upper segment is the inter-hyal, the long bar the epi-ceratohyal, and the short, distal segment the hypo-hyal.

In the lowest Urodele, *Proteus*, the hyoid arch is composed of two massive segments, one short, the upper or hyomandibular, and the other, the long, lower bar, the cerato-hyal; this is like that which obtains in Sharks.

In the larger Urodeles (*Menopoma*, *Cryptobranchus*) there is but little difference (apparently) in the time of development of the segments, but the upper part breaks up into two segments corresponding to the hyomandibular and symplectic segments in the Sturgeon; the cerato-hyal is large, and the hypo-hyal breaks up into three pieces.

In many of the Caducibranchiate Urodeles, and in some kinds of Anura (*Salamandra*, *Triton*, *Pseudophryne*, *Bombinator*), all but the uppermost part of the hyoid arch is suppressed; but in the Batrachia, generally, it is developed, as *two*, *three*, or even *four* segments; these, with the exception of the uppermost, as a rule, do not appear until two or three months after transformation, and are only developed in the Tadpole in rare cases, as in *Pseudis* and *Pipa*.

In *Lepidosteus* and in *Acipenser* the formation of the segments of the hyoid arch takes place at once during chondrification; *Lepidosteus* has the same number of cartilages as the Teleostei, but *Acipenser* has a distinct symplectic piece—a kind of segmentation which is not equivalent to the subdivision of the upper part of a branchial arch into a *pharyngo-* and an *epi-*branchial, but the epi-hyal is segmented at its distal fourth.

The basi-hyal of *Lepidosteus* is remarkable for being very long and essentially double. There are only four perfect and one imperfect branchial arches ; the auditory capsules, at first, are as distinct as in the Tadpole, their basal region remains membranous for a good while, as in the Salmon.

In embryos two-thirds of an inch in length, more than one-half larger than our first stage, the chondrocranium is larger and stronger, but has few fresh things in it.

The trabeculæ and palato-quadrate cartilages are still confluent, but the former are now some distance apart, the binding cells of the former stage being converted into a pyriform mass of true cartilage, with its broad end in front and projecting beyond the paired bands or trabeculæ ; this is the intertrabecula. The pedicle of the suspensorium has applied the inner side of its apex to the most curved part of the trabecula, and an oblong joint is forming.

A spike of cartilage has grown forwards from the auditory capsule over the hinder part of the superorbital region ; this structure is seen temporarily in large larvæ of *Triton*, and permanently in *Siren*.

The divergence of the basal bands is now at its fullest, and the apex of the cranial notochord—one-third of the rod—is twisted, curves a little upwards, and is far from the moieties of the investing mass.

In young *Lepidostei*, one-half larger than the last (1 inch long), the chondrocranium may be said to be complete, and free from intrinsic ossification, except in the sheath of the notochord, the cerato-hyal, and some parts of the branchial arches.

The whole structure is much longer, but most of the increase in length is due to the development of the three basal cartilages in front of the cranial cavity. The occipital arch is perfect, and the tegmen from it runs well forward.

The superorbital band is now perfect, and in front it passes into an anterior tegmen round the olfactory lobes, and the hemispheres, thus the cranial box is perfect there. But there is a large pyriform fontanelle below, a larger oval fontanelle on each side in the orbital region, and a still larger membranous space, the great fontanelle, above.

The sudden and immense development of the precranial bars in so short a time is very remarkable ; their relative massiveness makes this skull like that of a young Sturgeon five or six times as large. In that type the solid rostrum is formed of the two large trabecular cornua, which flank the still larger intertrabecula, like decurrent leaves. In the Sturgeon there is an antorbital expansion of the lateral ethmoidal region at the end of the rostrum, and each olfactory capsule lies close in front of the antorbital wall, as in a crypt. But in *Lepidosteus* the two capsules are carried away to near the end of the snout, and have no cartilage near them except the rostral bar, on each side of which they lie.

Whilst the fore part of the chrondrocranium is like that of a young Sturgeon 5 or 6 inches long, the cranium proper is like that of a Salmon ten or twelve days after hatching, when its length agrees with that of this stage of *Lepidosteus*, namely, about 1 inch.

In the Salmon "fry" there is a hinder and a front tegmen cranii, a pair of super-orbital bands running from the auditory capsules to the anterior tegmen, a largely open roof between, open orbito-sphenoidal spaces, and an open pituitary fontanelle. Moreover, this is the "norma" according to which the skull of *Polypterus* is formed; but of course during growth it becomes more solid, and partly ossified.

The suspensorium suggests a very mixed relationship in this type; it runs forwards, parallel with the skull, as in the Tadpole, but its pedicle is now well articulated with a basipterygoid process as in the metamorphosed Frog, and more clearly than in that type prefigures the cranio-facial relation of the Sauropsida, where, as in Lizards and many Birds, the pterygoid portion of the suspensorial apparatus articulates with a basipterygoid outgrowth of the skull. The open orbito-sphenoidal spaces are seen again in Batrachians, *e.g.*, in *Acris Pickeringii* and *Rappia bicolor*.

The palatine portion of the suspensorium (or palato-quadrate cartilage) loses its ethmoidal conjugation, but retains its continuity with the pterygoid cartilage. The primarily and permanently separate palatine of the "Siluroids" runs forwards in the same manner, with no ethmo-palatine joint, such as is seen in the Salmon.

In adult Batrachians of the genus *Bufo* the continuity of the palatine cartilage is lost both with the ethmoid and the pterygoid cartilage, but it articulates with the former by a raised process as in the Salmon. The small size of the hyomandibular of *Lepidosteus,* and its distance from the mandibular pier, prepare us for the transformations of that part in the Batrachia where it becomes the "columella."

In a further stage, when it has doubled the size it had in the last instance—has become 2 inches long—the young *Lepidosteus* has fairly attained to its own characteristic type of skull, and most of the very limited osseus centres are now apparent. All the fore face is now greatly drawn out, twice as much as in the last, and the suspensorium, mandible, and lingual cartilages, have shot on forwards in like manner. The membranous spaces are only different from the last by the upper fontanelle being relatively less, and neatly circular, whilst the lower space is being divided by a *late* and *feeble* "post-pituitary" bar with a large anterior, and a small posterior space. But the type of skull seen in the young "fry" of the Salmon, and in such minute arrested Frogs as the Nearctic *Acris Pickeringii*, and the Australian *Rappia bicolor* and *Camariolius tasmaniensis*, is not departed from, nor, indeed, will be.

But even what is seen in young *Lepidostei* 2 *inches* long scarcely prepares us for what we find in specimens a little more than twice that size. At this stage, as in Saw-fishes (*Pristis*), this prenasal cartilage (intertrabecula) has become *three times* as long as the whole cranial cavity, and *six times* as long as its associated cornua trabeculæ—now mere delicate leafy appendages to its base. The cranium proper has not altered in any important degree since the last stage, but the bony centres are nearly all there; all those that are seen in the Salmon, or in Teleostei, generally are found, with the exception of the super-occipital and a bone not found, I believe, in the Ganoids, namely, the "pterotic;" its suppression is correlated with the development of a special

temporal scute over the same region; the "squamosal," a bone only, exceptionally present in the Teleostei among the Siluroids.

The post-pituitary band of cartilage, a feeble promise of the solid post-clinoid wall of the "Amniota," is now complete. Some things characterising this type are now well seen, namely, the small lateral ethmoidal bone in the thin, closing-in, skull wall, without any prefrontal (ali-ethmoidal) wing, the double "articular" centre, and the huge coronoid crest to the articulo-Meckelian rod; these two latter characters are also seen in *Amia calva*, as shown by Professor BRIDGE.

The very small size of the preoperculars, the form and size of the interopercular, which here so strongly resembles the preopercular of the Teleostei, are very noticeable in this skull, as also the long chain of bones interspersed between the "os mystaceum" or edentulous maxillary and the premaxillary.

The adult condition of the skull in *Polypterus* and *Amia* (TRAQUAIR, Jour. of Anat. and Phys., vol. 5, plate 6, pp. 166–182; and BRIDGE, ibid., vol. 9, plate 23, pp. 605–622) presents so many things, both in likeness and contrast, that they must be noticed in conclusion.

In *Polypterus*, as in *Lepidosteus*, the four fontanelles are permanently open; the basioccipital projects far beyond the oblique foramen magnum, and the occipital bone is single, made up evidently of a basal and two lateral pieces, without a supraoccipital; then there are no pterotics, and the olfactory capsules are sub-terminal. But in this type there are no epiotics distinct from the opisthotics.

There is a large sphenotic bone, right and left, which takes up the antero-posterior sphenoidal regions and part of the lateral ethmoidal, besides which there is a pair of lateral ethmoidals which project outwards, and an ethmo-septal bone in front.

The metapterygoid in *Polypterus* is far from the skull, in which there are no basi-pterygoid processes; the palatine is a small ectosteal bone; the hyomandibular has only one centre; and the preopercular is continuous with the squamosal, as in the Amphibia; there is no interopercular.

But *Amia calva* has a skull which comes much nearer to that of *Lepidosteus* in several respects, but the lateral and inferior fontanelles are filled in, in this solid skull, which comes nearer that of the Physostomous Teleosteans.

The basioccipital projects behind the oblique foramen magnum; there is no supra-occipital, nor any pterotics, and the epiotics are distinct from the opisthotics.

It has a pair of bones which are not seen in *Lepidosteus*, namely, the orbito-sphenoids; and its so-called prefrontals or lateral ethmoids project, as in the Teleostei. It has a distinct pedicle to the suspensorium, capped with cartilage, but not forming a definite joint with any distinct basipterygoid.

Its palatine cartilage is ossified both endosteally and ectosteally; and the whole palato-pterygoid is almost Teleostean in its solidity.

There is a large coronoid crest, and there are *two* articular bones on each side, as in *Lepidosteus*. There is a cartilaginous inter-hyal, articulated between a distinct

hyomandibular and symplectic; and the upper or styloid end of the cerato-hyal has, as in Osseous Fishes, a separate centre, whilst the hypo-hyal has *only one*, as in *Lepidosteus*; in Osseous Fishes it has *two*.

There are the four normal operculars; the "os mystaceum" is dentigerous and carries a jugal in its hinder half. Above the skull, the scutes, which seem to me to be a little misunderstood by Professor Bridge, correspond, in essentials, to those of *Lepidosteus*.

I should propose the term "azygous parietal" for his *dermo*-superoccipital; "squamosals" for his *parietals;* and "prerostral" for the azygous transverse bone, which, as in *Lepidosteus*, furnishes the snout in front, and which is called by him *ethmoid*. The olfactory capsules are sub-terminal, and the large *nasals*, which cover them by their notched fore margin, are evidently the nasals and "ethmo-nasals" of *Lepidosteus*, in one piece, right and left.

Amia is a true Ganoid, and it has several unmistakable diagnostics even in its skull; but it comes very near to the Physostomous Teleosteans.

Description of the Plates.

Plate.	Fig.	Stage.		Number of times magnified.
30	1	1	Section of the head of an embryo of *Lepidosteus* 4 lines long	30
,,	2	1	A similar section of an embryo $4\frac{1}{2}$ lines long . .	30
,,	3	2	Chondrocranium of an embryo 5 lines long; lower view.	36
,,	4	2	Section of the head of an embryo $5\frac{1}{2}$ lines long .	30
,,	5	3	Section of the head of an embryo $7\frac{1}{2}$ lines long .	$22\frac{1}{2}$
,,	6		The other half of the same head	$22\frac{1}{2}$
,,	7	3	Chondrocranium of an embryo $\frac{2}{3}$-inch long; lower view.	30
,,	8	3	The same skull; upper view	30
,,	9	3	Head of same embryo; lower view	15
31	1–15	3	A series of vertically transverse sections through the head of an embryo $7\frac{1}{4}$ lines long	30
32	1	4	Chondrocranium of an embryo 1 inch long (nearly). Upper view	24
,,	2	4	The same object; lower view	24

Plate.	Fig.	Stage.		Number of times magnified.
32	3	4	Part of basis-cranii of same skull; upper view. .	36
,,	4	4	Section of the head of an embryo of the same stage .	24
,,	5	4	Upper view of head of same stage. Seen partly as a transparent object	24
,,	6	4	Part of hyoid arch of same	24
33	1–13	4	A series of vertically transverse section of an embryo, 1 inch long (nearly)	27
,,	14–16	5	First three of a series of vertically transverse sections of a young *Lepidosteus* $2\frac{1}{2}$ inches long .	20
34	1	5	Dissection of skull of young *Lepidosteus*, 2 inches long; chondrocranium with some of the parostoses attached; upper view	12
,,	2	5	The same object; lower view	12
,,	3	5	Part of basis cranii of same skull; upper view . .	15
,,	4	5	Inferior arches of the same skull	12
35	1–12	5	4th to 15th of a series of vertically transverse sections of a young *Lepidosteus*, $2\frac{1}{2}$ inches long.	20
36	1–8	5	16th to 23rd of a series of vertically transverse sections of a young *Lepidosteus*, $2\frac{1}{2}$ inches long.	20
,,	9	5	Part of fig. 8	60
37	1	6	Skull of a young *Lepidosteus* 4 inches 5 lines long, with superficial bones *in situ*; side view . . .	6
,,	2	6	The same skull; upper view.	6
,,	3	6	The same; lower view.	6
,,	4	6	The inferior arches of the same skull; outer view .	$7\frac{1}{2}$
38	1	6	Chondrocranium of a young *Lepidosteus* 4 inches 5 lines long; upper view	$6\frac{3}{4}$
,,	2	6	Hind part of same; lower view	$6\frac{3}{4}$
,,	3	6	Part of basis-cranii of same; upper view . . .	$13\frac{1}{2}$
,,	4	6	Part of chondrocranium of same; upper view . .	$13\frac{1}{2}$
,,	5	6	Inferior arches of the same skull; inner view . .	$7\frac{1}{2}$

List of Abbreviations.

The Roman figures indicate nerves or their foramina.

ag. Angular.
al.s. Alisphenoid.
ar. Articular.
ar.c. Articular cartilage.
a.s.c. Anterior semicircular canal.
au. Auditory capsule.
au.f. Auditory fenestra.
b.a. Basilar artery.
b.br. Basi-branchial.
b.hy. Basi-hyal.
b.o. Basioccipital.
b.pg. Basipterygoid.
C^1. Fore brain.
C^2. Mid brain.
C^3. Hind brain.
c.br. Cerato-branchial.
c.hy. Cerato-hyal.
cl. Cleft.
cr. Coronoid.
cr.c. Coronoid cartilage.
c.tr. Cornua trabeculæ.
d. Dentary.
e. Eye.
e.br. Epi-branchial.
e.hy. Epi-hyal.
ep. Epiotic.
et.n. Ethmonasal.
f. Frontal.
fo. Fontanelle.
g.p. and *br.p.* Gill processes.
h. Heart.
h.br. Hypo-branchial.
h.hy. Hypo-hyal.
hm. Hyomandibular.
hm.c. Hyomandibular facet and condyle.
hm.f. Hyomandibular fenestra.
h.s.c. Horizontal semicircular canal.
i.hy. Inter-hyal.
inf. Infundibulum.
i.op. Interopercular.
i.tr. Intertrabecula.
j. Jugal.
l.eth. Lateral ethmoid.
m. Mouth.
m.c.g. and *m.g.* Mucous gland.
mk. Meckel's cartilage.
mn. Mandible.
ms.pg. Mesopterygoid.
mt.pg. Metapterygoid.
mx'., *mx.''* Maxillary.
my. Myelon.
n. Nasal.
nc. Notochord.
ol. Olfactory capsule.
op. Opercular and opisthotic.
op.p. Opercular process.
os.f. Orbito-sphenoidal fenestra.
ot.p. Otic process.
p. Parietal.
pa'. Superficial palatine.
pa.s. Parasphenoid.
p.br. Pharyngo-branchial.
p.cl. Posterior clinoid.
pd. Pedicle.
pg. Pterygoid.
pnl. Pineal gland.
p.ob. Preorbital.
p.op. Preopercular.
p.pg. Palato-pterygoid.
p.px. Palatine process of premaxillary.
pr.o. Prootic.

pt.o.	Postorbital
px.	Premaxillary.
py.	Pituitary body and space.
q.	Quadrate.
q.c.	Quadrate condyle.
s.ag.	Supra-angular.
s.d.	Sucking disk.
spl.	Splenial.
s.ob.	Supraorbital.
s.ob.c. and *s.ob.*	Supraorbital cartilage.
s.op.	Subopercular.
sp.o.	Sphenotic.
s.t.	Supratemporal.
su.ob.	Suborbital.
sy.	Symplectic.
t.cr.	Tegmen cranii.
tr.	Trabecula.
v.	Vomer.
vb.	Vestibule.

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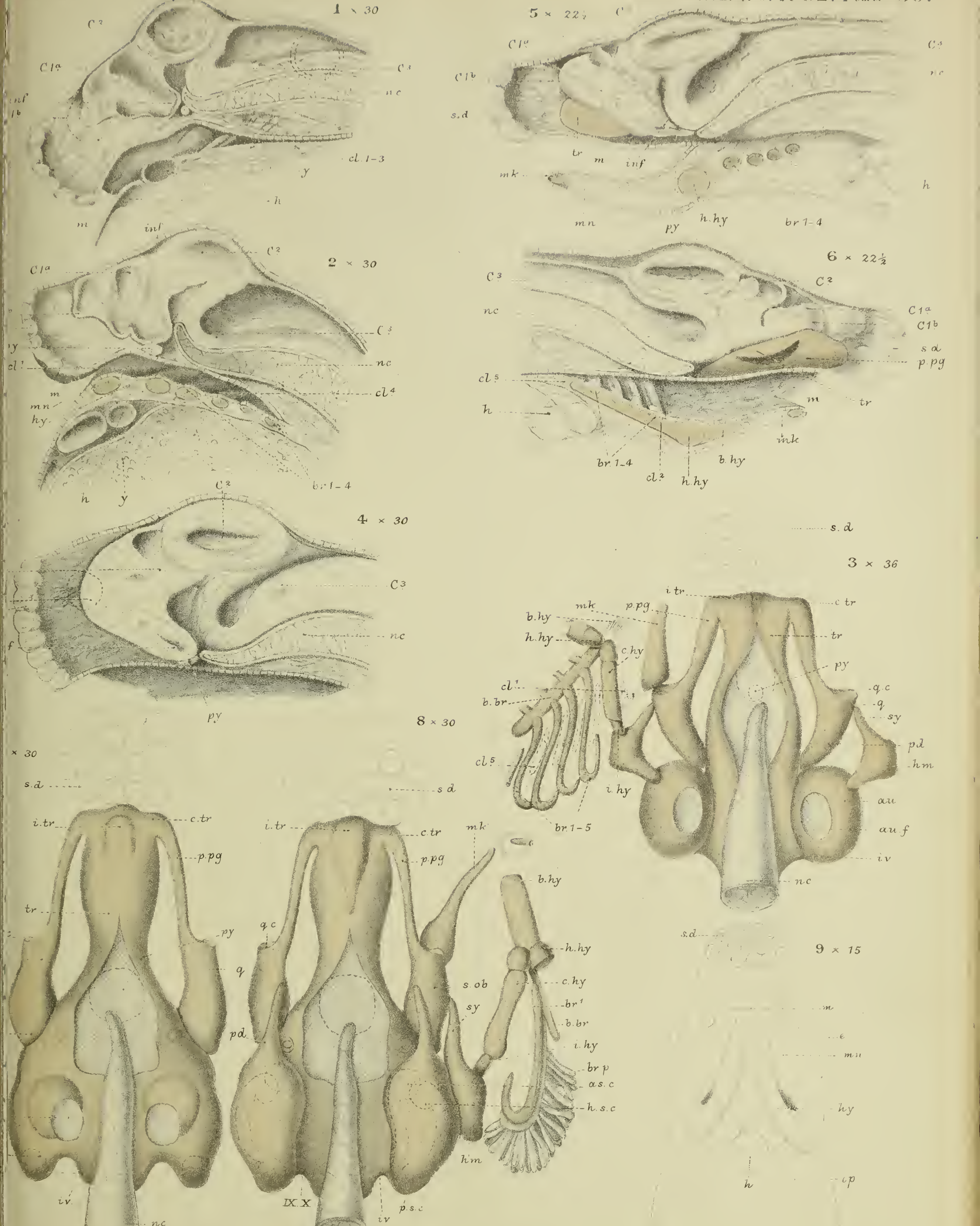

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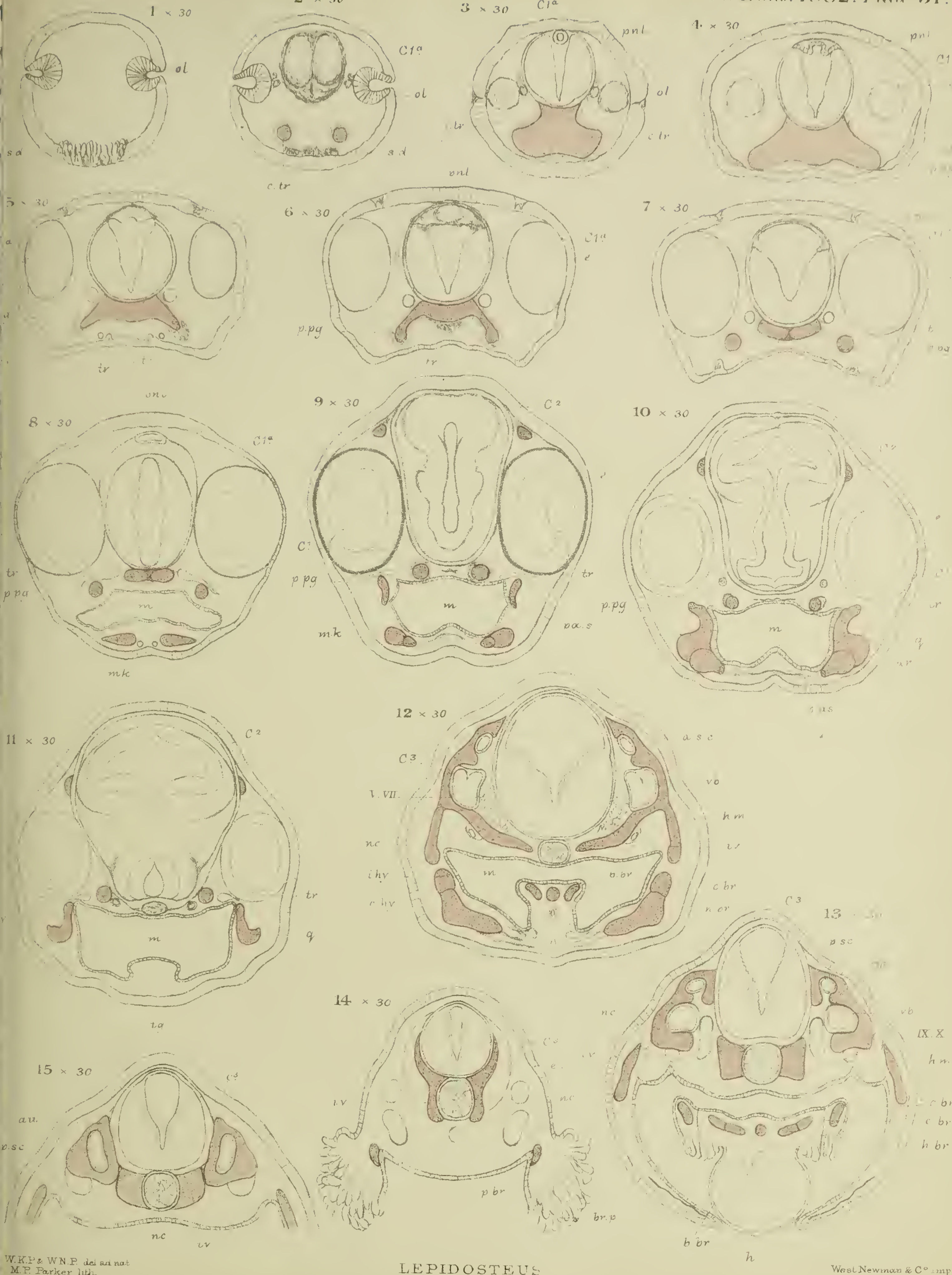

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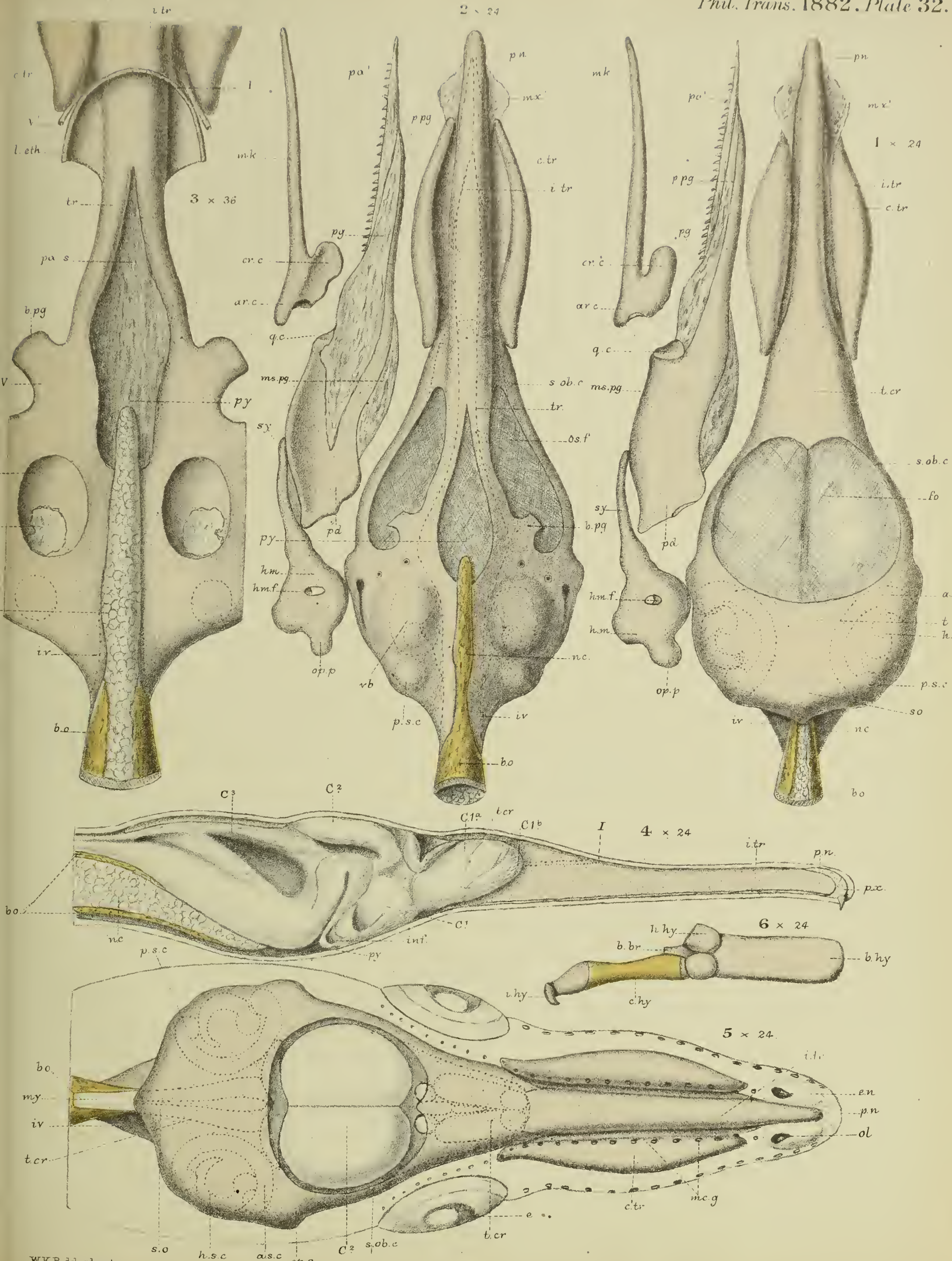

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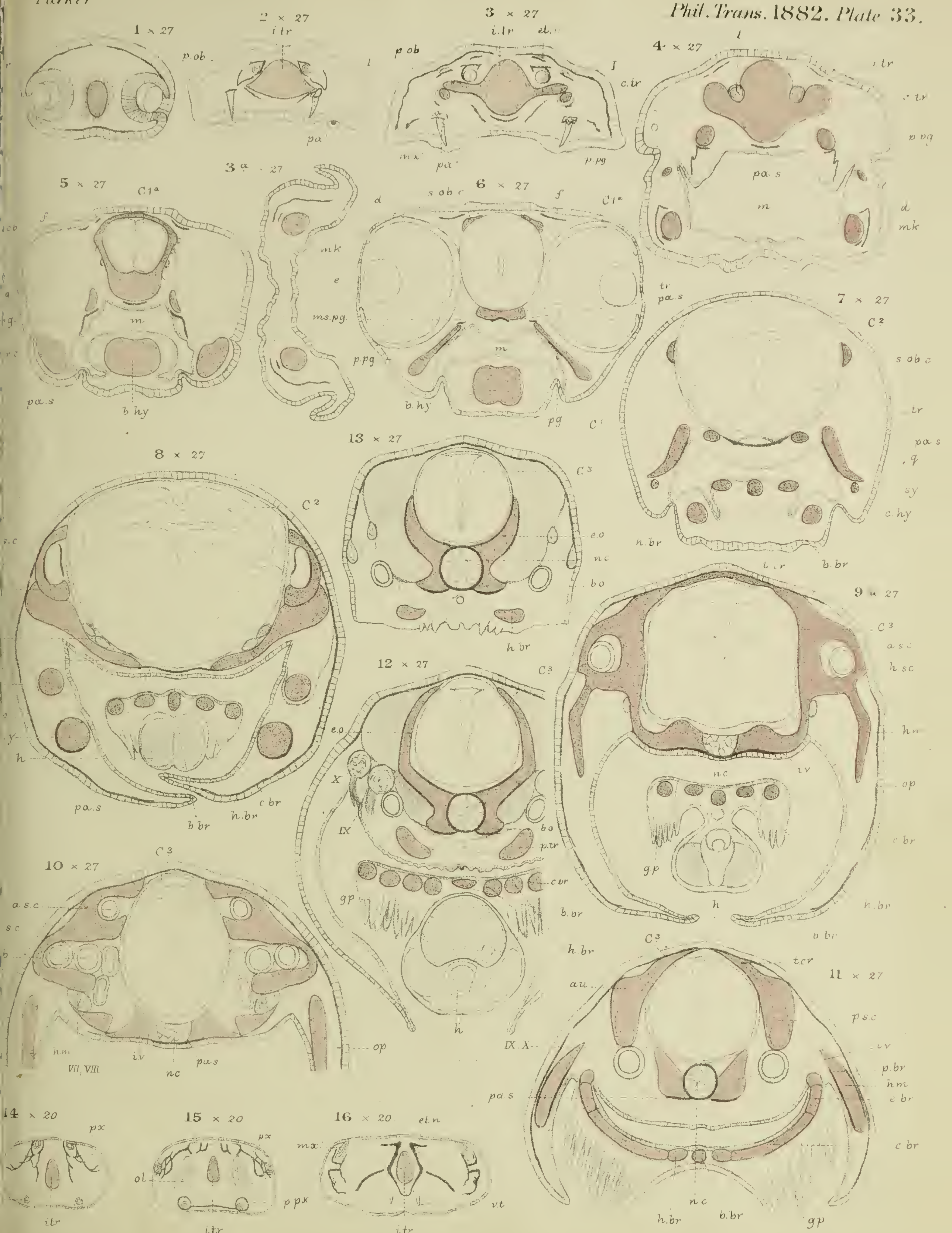

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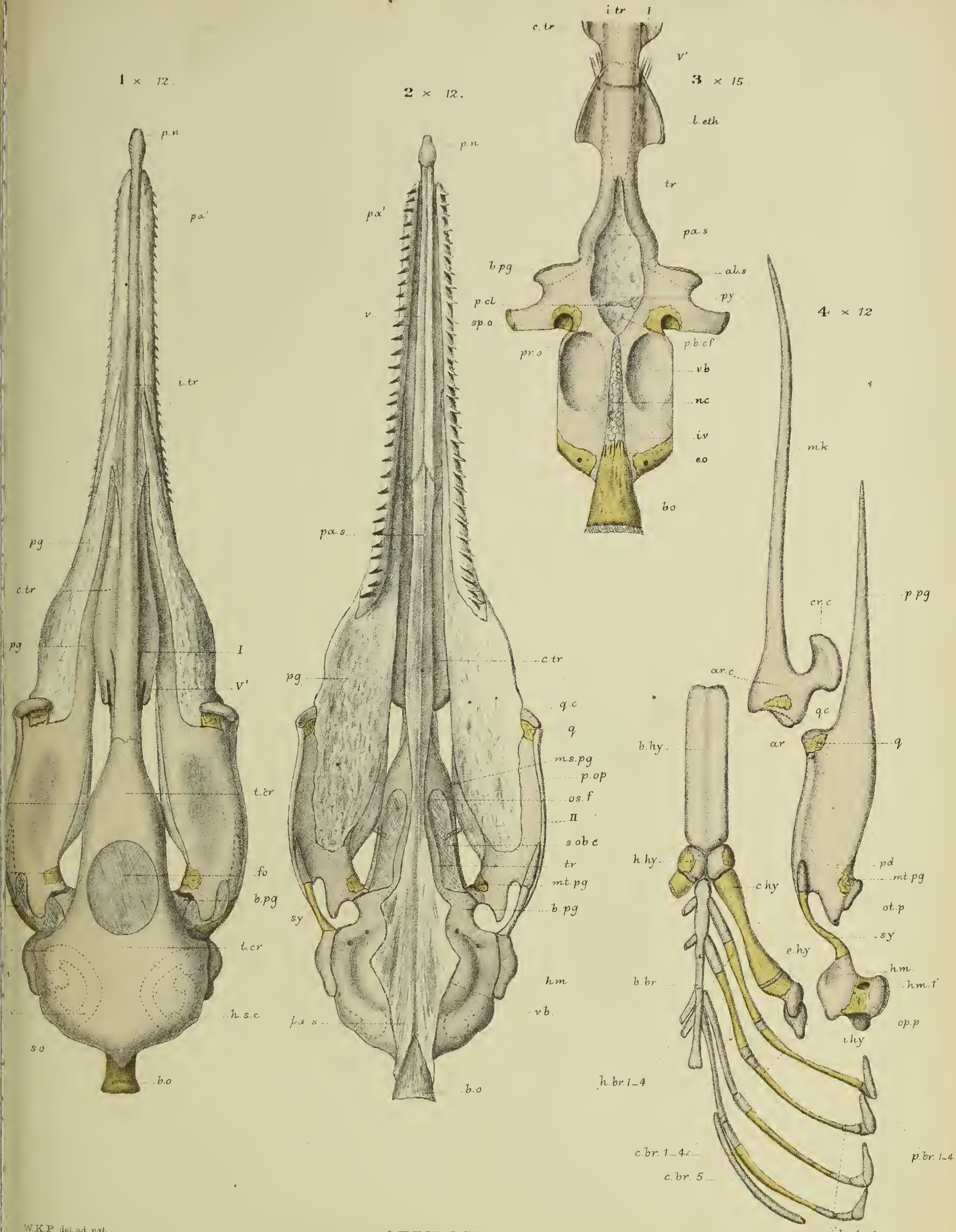

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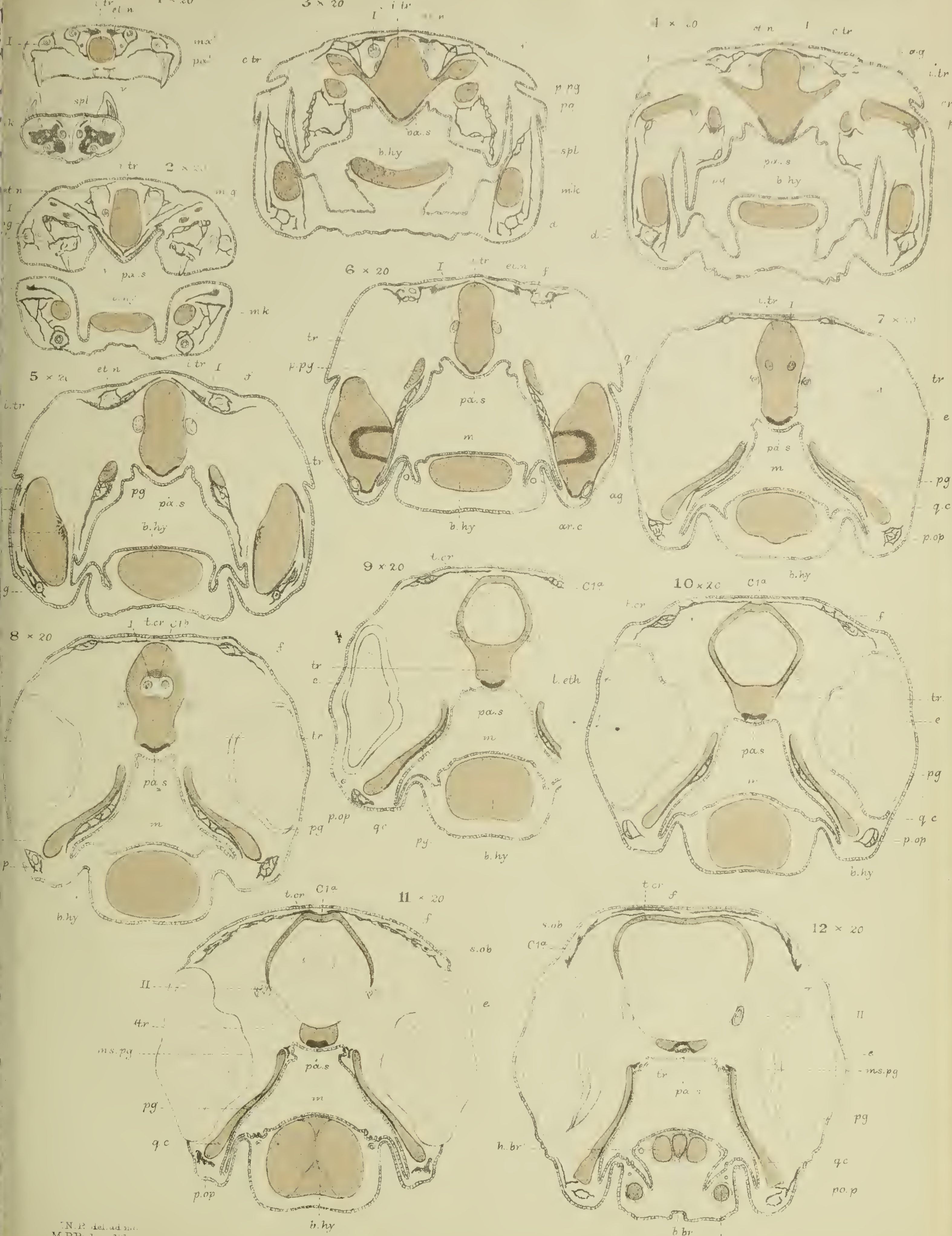

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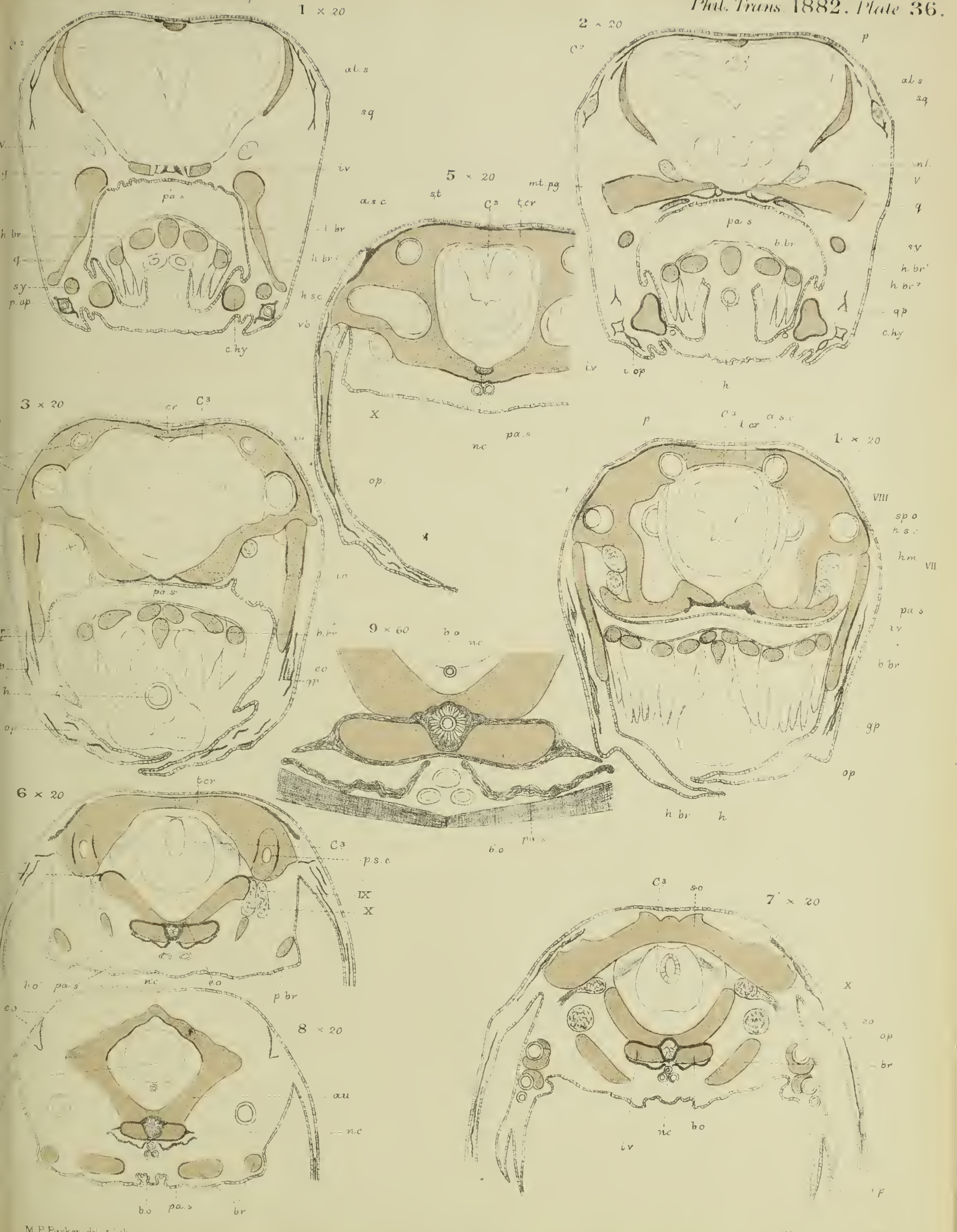

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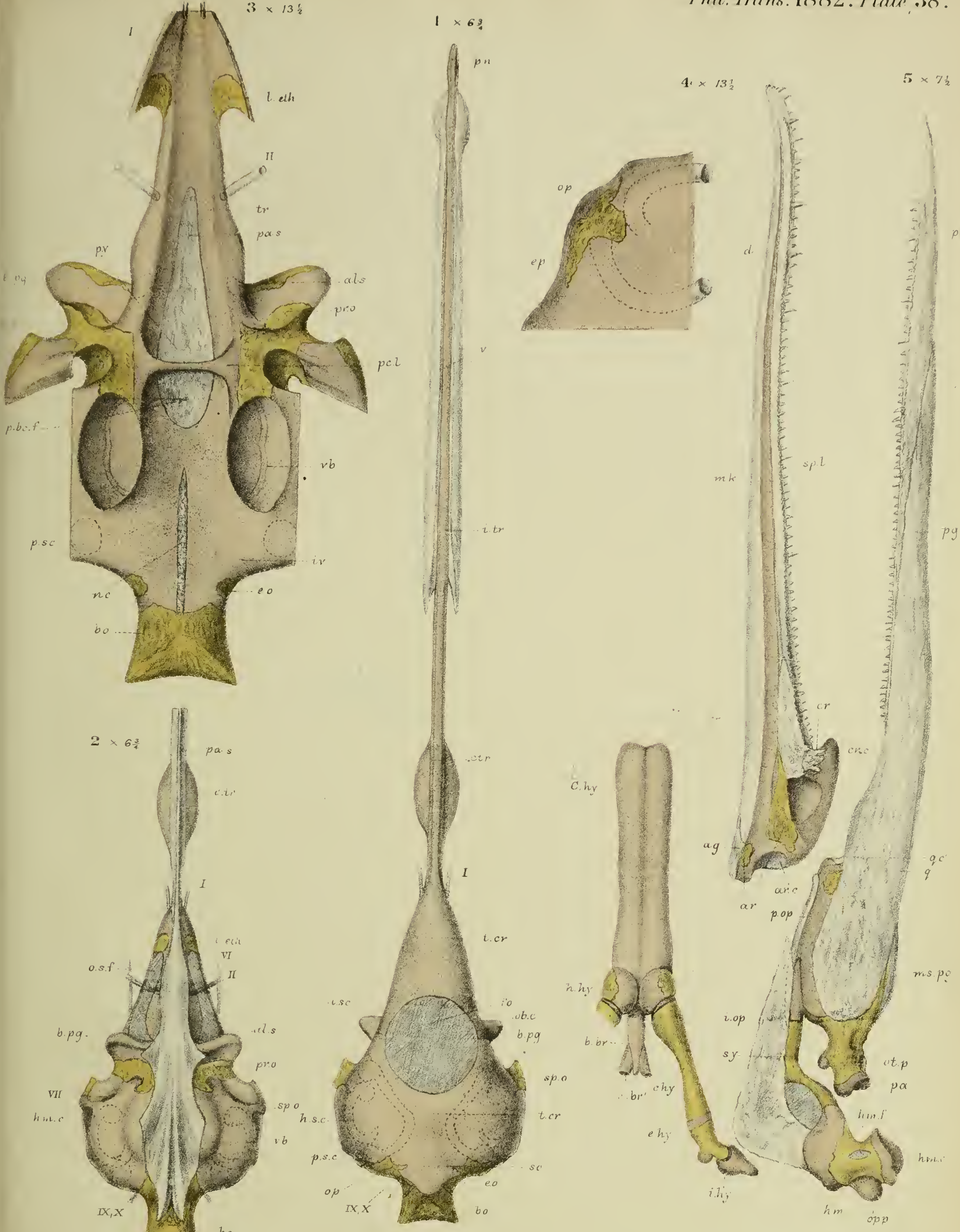

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II. The Bakerian Lecture.—*On the Structure and Development of the Skull in the Salmon* (Salmo salar, *L.*). *By* William Kitchen Parker, *F.R.S.*

Received April 18,—Read May 30, 1872.

Introductory Remarks.

At the close of my last communication, on the Frog's Skull, I promised to bring forward a paper on that of the Salmon; indeed the present paper should have appeared next after my memoir on the Skull of the Fowl (see Phil. Trans. 1869, p. 804); but the invaluable labours of my friend Professor Huxley on the "face" of the Vertebrata (see Proc. Zool. Soc. 1869, pp. 391–407) deflected me for the time, and I was led to labour at the Amphibia. This new subject has been fraught with as much pleasure as the one before it; for although the Salmon begins as a *higher type* and ends as a *lower* than the Frog, yet it also undergoes no little metamorphosis, and its transformations are not a whit less instructive than those of the Frog. Moreover, let this be said in praise of this fish, that its eggs and its fry are the most exquisite objects the morphological observer can ever hope to spend his time upon—their size and their diaphanous character making them excellent subjects for section, dissection, and viewing under any and every degree of magnifying-power. As to the source of these specimens, it is due to the donors that their names should be mentioned here; they are my friends Messrs. B. Waterhouse Hawkins, Frank Buckland, and Henry Lee, who have most kindly put every valuable specimen into my hands that I have desired, not only for this paper, but for others completed, in hand, or in prospect.

Cuvier must be taken as the great pioneer in this branch of Ichthyotomy; many of his determinations are excellent, yet, from his not having worked out the development of the Fish, several of his terms are not defensible.

My own earlier study of the Fish's skull was assisted by Professor Owen's well-known 'Lectures on the Vertebrata' (vol. ii.); his modification of the Cuvierian nomenclature is very elegant and useful. Of course the determination of homologies will differ largely when one worker looks at them from the transcendental stand-point, whilst another creeps up to them from below, caring only to see them in the light of development: my divergence from this "guide" was soon to take place.

Professor Huxley's Croonian Lecture, delivered before the Royal Society on June the 17th, 1858, gave a painful but healthy shock to my mind; having learned that the whole subject had been begun from the wrong end, it took some time to acquire calmness and courage to begin afresh. Help, however, came in time; and the same author threw

much new light upon this difficult subject in his Hunterian Lectures, delivered at the Royal College of Surgeons of England in 1863.

During that time, and since then, this subject has been frequently and warmly discussed between Professor HUXLEY and myself; although all that I have written hitherto upon Ichthyotomy has been incidental and in elucidation of higher types, yet, with the exception of the Bird-class, the Fishes have received most of my attention.

In the present paper the nomenclature will be based upon CUVIER'S, as modified and made elegant by OWEN and as corrected by HUXLEY. I shall, however, have to differ on several points from the last of these three anatomists.

The most invaluable part of Professor HUXLEY'S labours is that which has given us the true auditory elements in the bony skeleton; three of these are almost universal—namely, the "prootic," the "opisthotic," and the "epiotic." CUVIER only recognized the second of these as necessary to the "pars petrosa," his "rocher;" the prootic was mistaken by him for the "great wing of the sphenoid," and the epiotic as part of the occipital arch, his "external occipital." But CUVIER, and OWEN after him, were right in putting another element, their "mastoid," amongst the auditory centres; and Professor HUXLEY was wrong in supposing this piece to be the "squamosal." I pointed out this error to him before his Lectures were in print; but he was doubtful about what I had long felt certain of, and called it my *opinion* (see note to p. 188 in his Elem. Comp. Anat.). In his new work, however ('Anatomy of the Vertebrated Animals,' 1871, p. 153), this bone is put into its proper category: thus we have *four* "periotic" bony centres. I now have to speak of another periotic bone, the nature of which I have long pondered over, namely the "postfrontal." This bone, which was so called by CUVIER, but has nothing in common with his Reptilian postfrontal (a mere postorbital investing plate), begins as a delicate tract of osteoblasts immediately outside the ampulla of the anterior semicircular canal; another ossifying tract begins over the ampulla and arch of the horizontal canal, this is the "pterotic;" a third over the ampulla of the posterior canal, this is the "opisthotic;" a fourth over the arch of that canal, the "epiotic;" whilst the fore edge of the periotic capsule is ossified by the "prootic." I thus anticipate my descriptions for the sake of starting fair in my terminology; I propose the term "sphenotic" for the antero-superior or postfrontal bony centre.

As soon as possible all the terms must be put into harmony with the facts of morphology, and terms that are applied to two different parts in different Classes must be got rid of if they can conveniently be spared. Thus the term prefrontal, which is applied to a mere investing bone in one case and to the lateral mass of the ethmoid in another, ought to give way, in one case to preorbital, and in the other to a true morphological term, namely "ecto-ethmoid."

I have long ceased to use such terms as "os transversum," "ectopterygoid," and "entopterygoid," as they do not mean the same thing in the Fish as in the "Sauropsida" and the Mammalia. CUVIER'S "transverse" of the Fish is really the pterygoid, as Professor OWEN has well shown: Professor HUXLEY calls it "ectopterygoid;" whilst his ento-

pterygoid (the Owenian name in this case, and answering to the internal "pterygoid" of CUVIER) does not answer to the internal pterygoid plate of Man and the other Mammalia, but to an additional bone occasionally seen even in them. By adopting the term "transpalatine" for the Reptilian transverse bone, "pterygoid" for the homologue of our internal pterygoid plate, and "mesopterygoid" for the innermost or submesial plate, I seem to myself to have struggled out of a quagmire of obstructive terms on to something like a raised causeway.

Many specially ichthyotomical terms must be retained, such as "hyomandibular," "symplectic," and the like; for although we now begin to see what the representatives of these bars are transformed into in the higher classes, yet they have in their more primitive condition in the Fish an essentially specific character as morphological elements; whilst their metamorphosed counterparts in the higher types may be compared to new species, developed during secular periods.

In my last paper I stated my opinion as to the merely *varietal* value of the bony deposits that take place in the general connective web; these bony plates may be *superficial*, *intermediate*, or *deep*, the latter mostly fastening themselves on to cartilaginous tracts, and causing their transformation into true bone.

We have three groups of such bones—namely, "dermostoses," "parostoses," and "ectostoses:" in the Teleostei, as a rule, there are no "endosteal" deposits, or direct calcification of cartilage-cells, such as we see in Sharks, Rays, and in the "Anoura;" in the Salmon there are no "dermostoses" nor "endostoses."

If the reader will refer to the figures of *Callichthys* (a Teleostean covered with Ganoid armour) in my memoir 'On the Shoulder-girdle,' he will see how gently and almost insensibly the body-plates pass into the armour for the head; this is the first degree of specialization in relation to the cephalic endoskeleton. A further degree is obtained by the ossific deposit being found in a deeper stratum, the skin itself becoming the seat of deposits that form the proper scales of the fish, unrelated to the cartilage beneath; this we see in most Teleostei.

Let this be held in mind, and then all those bony plates in the Salmon's head which do not engraft themselves upon the cartilaginous skull and face can be arranged into one category—the splints, or "parostoses."

The deeper strata of bony deposit, on account of their peculiar behaviour correlative to the endoskeleton as "ectosteal" laminæ, are, as it were, taken into the very body and substance of the endoskeleton, and become part and parcel of it; they may be called *secondary endoskeletal elements*, in contradistinction to the parts into which they grow, which are *primary*.

Thus in morphological species, as well as zoological, there is frequently a dovetailing of members, a mutual trespassing of territories; and the sharp boundaries, which for the sake of logical clearness we are always drawing out, often belong to us, as intellectual conceptions, rather than to Nature, as solid and tangible facts.

Before concluding these remarks I must express my gratitude to Dr. TRAQUAIR for

his excellent paper on the *Polypterus* ('Journal of Anatomy and Physiology,' vol. v.); it has helped me greatly, beautifully showing the meaning of the earlier "Ganoid" stage of the Salmon's skull.

Structure of the Adult Salmon's Skull.—Eighth Stage.

I begin with the adult, and this because of the multiplicity of parts in the Teleostean skull: he has mastered no easy piece of work who knows these parts and their relations.

On the upper surface of the Salmon's skull there are five important parastoses—namely, the "superethmoidal," the frontals, and the parietals (Plate VII. fig. 1, *eth.*, *f.*, *p.*).

The parietals (*p.*) are small, ridged, subarcuate bones, separated by the whole width of the broad supraoccipital (*s.o.*); they articulate with it, and also with the corresponding frontal (*f.*) and with the epiotic (*ep.*); their relation to the ossified and unossified skull proper is shown in section (Plate VIII. fig. 6, *p.*, *s.o.*).

The frontals (*f.*) are, as is usual in the Teleostei, very large; they only meet to form the sagittal suture in their hinder half, for further forwards the smooth strong ridge of the cartilaginous skull separates them. They rise thin towards the edge, and at the base of this ascending lamina there is a considerable sulcus, outside of which they expand to an equal size again in front, and to twice the width behind. The fore and outer part is leafy and jagged, so is the hinder half at its extreme width, in its supraorbital portion; but the rest is a thick bed of excavations for fatty tissue. The exact relation of the frontals to the skull proper is shown in a series of transverse sections (Plate VII. figs. 8–11, and Plate VIII. figs. 4 & 5, *f.*).

The character of the frontal roofing is well shown by the effect produced and the parts exposed when these bones are removed (compare Plate VII. fig. 1 with Plate VIII. fig. 1).

The fore part of the cartilaginous skull is covered in by a bone (Plate VII. fig. 1, *eth.*) which has been the subject of much discussion; and here the Salmon shows itself to be a halfway type between the typical Teleostei and the Ganoids.

In the "Siluroids," for instance *Callichthys* and *Clarias* (see for the latter, HUXLEY, Mem. of Geol. Surv. decade 10th, 1861, p. 30, fig. 20, *eth.*), there is a large Ganoid scale in this region, similar to what is found in *Coccosteus* (*op. cit.* p. 30, fig. 19, *eth.*). Now in the "Siluroids" the dermal scute has coalesced with a true meso-ethmoidal bone, formed by an ectostosis; but in the Salmon that region of the skull is entirely unossified, and the bony plate is parosteal. In another malacopterous fish, the Pike (*Esox lucius*), there are two ossifications in the meso-ethmoidal cartilage, one on each side in front (see HUXLEY, 'Elem.' p. 186, figs. 7. 3, A, B, C 3), and the long, flat snout is overlain by a pair of parostoses (*op. cit.* p. 168, fig. 69. 2). Then in other Malacopteri, namely, the "Cyprinoids," there is a proper median ossification of the meso-ethmoidal cartilage (see HUXLEY, Croon. Lect. p. 24, fig. 6, *eth.*); and this is the state of things in the "Acanthopteri" (e. g. *Zeus*) and the "Anacanthini (e. g. *Gadus*). In the "Ganoid" *Polypterus*, the median, proper meso-ethmoidal bone is invested by a pair of large ganoid

plates (TRAQUAIR, Journ. Anat. and Phys. vol. v. figs. 1, 2, 3, 7, *na.*); these are supplemented by an additional pair (*na'.*). The nasal sac itself has a small roof-bone, lettered *o.t.* (*os terminale*) in Dr. TRAQUAIR'S figure. In MÜLLER'S figure of *Polypterus*, as quoted by HUXLEY, *op. cit.* p. 22, the main superethmoidal plates are lettered *N.* It is evident, therefore, that there are several candidates in the *Polypterus* for homology with the human nasal bones. In the Fishes generally I retain the term "nasal" for the "os terminale" (the so-called "turbinal" of OWEN), which is the foremost of the upper fork of the "lateral-line" series of mucous bones, and which covers the nasal sac. This bone is shown in the Salmon in Plate VI. fig. 1, *n.*; it belongs to the same category as the superorbital (*s.o.b.*). These investments of the nasal region have merely to be regarded as a commencing specialization of the dermal scutes in relation to more and more metamorphosed ethmoidal structures.

Two large splints, one very large, invest the basis cranii; one of these has been known for many centuries in its mammalian form; it is the vomer (Plate VII. fig. 2, *v.*). This is an oblong bar of bone, thick in front; it sends upwards a sharp keel on this anterior portion, between the halves of the ethmoid (Plate VII. fig. 5, *v.*); behind, it is carinate downwards (Plate VII. fig. 7), and it is armed with sharp recurved teeth. This bone underlies the next for a considerable distance (Plate VII. figs. 2, 7, 8, *v.*, *pa.s.*). The next bone, by its primordial condition, characterizes the Ganoid and Teleostean Fishes and the Amphibia, although I find few even of the higher Vertebrata without traces of it; it is largest in the lower Ganoids, for instance the Sturgeon. A good Ichthyopsidan name was first given to it, "parasphenoid," by Professor HUXLEY (see Elem. p. 170); it is a submucous bone, intimately related to the basis cranii, and is of great length (see Plate VII. figs. 2 & 4, *pa.s*). This bone is large, a long leaf, with descending laminæ, and is split in front. It is also split behind into several snags, and from its hinder third sends upwards "basitemporal wings." It is upwardly keeled in front, downwardly keeled behind, and flattened in the middle (see sections, Plate VII. fig. 7–11, & Plate VIII. figs. 4–6, *pa.s.*). A view of the basis cranii after these two parastoses have been removed (Plate VIII. fig. 2) is instructive as to their architectural value.

The lateral-line series does not give us any conspicuous "supratemporals;" but there is one attached to the "pterotic" which is worth description; it is shown in Plate VI. fig. 1, *s.t.* This curved, rod-shaped mucous bone is articulated below to a large falcate bone full of gland-burrows, but this is formed in the proximal part of the opercular fold; it is the "præopercular:" hence it is evident that the slime-canals do not confine themselves to the two forks of the lateral-line series.

Over the eye there is one "superorbital," and under the eye two thirds of a ring of "suborbitals" (Plate VI. fig. 1, *s.o.b.*, *su.o.*); these are thick and strong-rimmed where they contain the glands, thin and splintery at the outer edge. The suborbitals are developed in the superior edge of the subocular bar, external to the cartilage.

The bones of the upper jaw show the aberrant or subtypical character of the Salmon, the maxillary being dentigerous as well as the intermaxillary. The latter (Plate VI.

fig. 1, *p.mx.*) is much the most massive and broad bone of the two; it has a nasal and a dentary region, and its structure is peculiarly sponge-like and tubuliferous.

The maxillary (*mx.*) is scooped where it is overlapped by the intermaxillary; it sends inwards a scooped facet for articulation with the palatine (*pa.*), is rod-like in its dentigerous portion, and flattens out below, especially on the upper edge, which is overlapped by the malar or jugal. This third bone (Plate VI. fig. 1, *j.*) is lanceolate, scale-like, and fimbriated above, like the down-turned end of the maxillary; it is only loosely connected with the hinge-work of the mandible.

A very large splint covers the anterior two thirds of the cartilaginous mandible, largely on the outer, and less on its inner side: this is the dentary (*d.*). The fore end of its tooth-bearing part is strongly hooked; and this hooking of the mandible, so as to fit into the fore end of the beak, gives a peculiar character to the Salmon's face, especially in old males. On the angle of the mandible another splint is found, the angulare (*ag.*); it is small and rough. But the most characteristic bones investing the skull and face are those which form the gill-cover; these attain their highest development in the Teleostei. There are two sets, the "opercular" and the "branchiostegal;" for the second postoral arch, from which the primary opercular fold is developed, splits into a twin-series of pieces at an early stage of growth. In the Ganoids, even in the Sturgeon, three of the four very constant opercular pieces are found on each side; in these the "præopercular" or proximal bone is not differentiated, and in the *Polypterus* (see TRAQUAIR, *op. cit.* plate vi. fig. 7, *y.*) the præopercular is one with a large "temporal," as in the Frog and Ostrich. This single representative of the "squamosal" and the "præopercular" is, in the *Polypterus*, burrowed by mucous glands"*.

The "præopercular" of the Salmon is quite subcutaneous; it has the usual falcate form, is burrowed in a radiating manner by mucous glands; its attachment is by its fore edge, above to the hinder edge of the hyomandibular, and below to that of the quadrate (Plate VI. fig. 1, *p.op.*, *h.m*, *q.*).

Another piece developed in the proximal edge of the opercular fold is the interopercular (Plate VI. fig. 1, *i.op.*); it is ear-shaped, its narrow end passing within the præopercular is very thin, and it is marked concentrically and radially by *growth-lines*.

The most constant of these bones in the "Ganoids" is the "principal opercular;" it is the cephalic counterpart of those scutes which lie directly below the mucous bones (see 'Shoulder-girdle and Sternum,' plate i. fig. 9, *op.*), and the next plate behind it belongs to the trunk and is related to the shoulder-girdle as the "supraclavicle." The "opercular" is a large subquadrate bone in the Salmon (Plate VI. fig. 1, *op.*); it is elegantly marked with both kinds of growth-lines, and it articulates by its own cup with a ball on the hyomandibular,—that process which is the morphological counterpart of the

* I purposely mention the condition of the opercular bones in *Polypterus*, and that for two reasons—namely, to trace the Teleostean bones in each case to their simpler Ganoid representatives, and to incite Professor HUXLEY to reexamine his lettering in the woodcut in his Geological Survey Memoir (p. 22, figs. 16 & 17, H.M., S.T.).

"extrastapedial" in the Anurous Amphibia and in the Sauropsida. The bone lying below and somewhat within the opercular is the "subopercular" (Plate VI. fig. 1, *s.op.*); it is subfalcate, broad in front, very thin, and is elegantly marked by growth-lines. Together these four bones form the framework to the great outer and upper gill-valve in the osseous fishes; they are there subcutaneous bones, although they are represented by true cartilages in the "Plagiostomes;" and the principal opercular piece is also represented by a cartilaginous sickle in the young Frog; it becomes, as I have already shown, the Batrachian "annulus tympanicus" ("Skull of Frog," Plate VIII. fig. 7, *a.t.*).

Along the infero-posterior division of the second postoral arch there are twelve rays on each side (Plate VI. fig. 1, *br.s.*); these are flat, thin, and shaped like a knife-blade; their attachment is to the lower margin of the "epiceratohyal" bar on its outer side. These rays decrease in size from above downwards; they form one continuous series: in Teleostei generally, especially the Acanthopteri and Anacanthini, there are seven on each side; these are terete rods, arranged in two groups—the upper four attached to the outside; and the three lower end to the inside of the hyoid cornu. Here, again, the Salmon is seen to be only subtypical. There is an azygous bone at the base of this series (Plate VI. figs. 1 & 5, *b.br.s*); it is the ossification of intermuscular septa, and forms a sort of *isthmus*; it does not answer to the "uro-hyal" of the Bird, which corresponds to the "basibranchial" bar of the gill-bearing tribe, but should rank with the lateral rays and be called the "basibranchiostegal." Nearly twice as many rays proceed from the first branchial arch (Plate VI. fig. 3); these are pointed, flattened, arcuate ossicles, attached to the fore edge of the branchial bar; their direction is forwards and a little inwards. There is a single row of them on the first and fourth arches, but there are two rows on the second and third arches (fig. 4); these are so arranged as to form a *colander* through which the water is strained, as it is incessantly sent through the branchial clefts. In the Tadpole, as I have recently shown, similar structures commence on the branchial arches, which become conical elevations of cellular tissue, densely covered with tufted branchiæ, and they serve both for straining and for respiration. In the typical Teleostei they only partially grow into bony rays even on the first arch, but form little mounds covered with bristling teeth. The merely fibrous bones are thus easily classified by considering their relation to the parts beneath; they belong to the skin and its multifarious ingrowths; the osseous matter has ceased to be formed from their outer surface, leaving the skin thoroughly differentiated from the skeleton within. These parts have attained a higher morphological condition than in the "Ganoids;" but they cease at this, their culminating point, and do not reappear, many of them, at least, even in the metamorphic "Ichthyopsida." Those bones, however, which do reappear in the higher classes become very constant, and are never lost sight of again even in our upward march to Man.

The bony plates now to be considered (the *deep* laminæ) possess a peculiar metamorphic potency; for wherever they fasten themselves upon a cartilaginous rod or

plate they, as it were, devour it, and convert it into their own substance; they have to be considered in connexion with the tracts of hyaline cartilage, which they are ever tending to obliterate.

The skull and face proper, deprived of the investing bones, is a very complex structure, a box above and a crate below; the two divisions will be best understood by considering them apart.

And first the box itself (see Plate VIII. figs. 1, 2, & 8), which is a compound structure, formed behind of axial parts, and before of facial. But, besides the axial and facial elements, there is to be considered how much is due to what the great ear-sacs superadd, and also what is superadded by the facial elements to the nose-sacs, which help to build their crypts; the eye-sacs are free, but are attached by a short cartilaginous pedicle (Plate VII. fig 3, *o.pd.*). There is one part of the skeleton which is truly azygous; and this is a primary, fundamental part, a part to which all the axial structures apply themselves; this is the "notochord." In the adult skull there is only one bone formed upon this fundamental part, the basioccipital; but the bony sheath of this axis acts upon symmetrical cartilages that appear very early, one on each side of the notochord; these are called, together, the "investing mass." This "investing mass" is the direct continuation of that part of the embryo which is so early segmented into the vertebral rudiments, yet itself, still closely embracing the azygous axis, is under the controlling influence of some force which prevents further segmentation. A quasi-vertebral ring or arch is, however, formed, the "occipital arch" (Plate VIII. figs. 1, 2, 7, 8); and this ring, seen from behind (fig. 8), has all the appearance and many of the characters of a vertebra. Only four of the bones seen from behind belong to this segment, the basioccipital (*b.o.*), the "exoccipitals" (*e.o.*), and the "superoccipital" (*s.o*): the three outermost pairs belong to the auditory capsule; they are "otic elements." But the "basioccipital" bone does not utilize all the "investing mass;" the notochord retires during growth, and the rest of the investing mass is ossified (not thoroughly) by the foremost of the otic bones, the "prootics." One remarkable change in the investing mass, as a whole, is the growth downwards of a lamella on each side, thus forming a covered archway; for in front of the retiring notochord the moieties of cartilage meet, and this viaduct is floored by the submucous bone which has been removed (Plate VIII. fig. 2), the "parasphenoid." All the true axial parts of the skull cease at the fore edge of the investing mass behind the pituitary space (*py.*); all the rest has a facial foundation, is built on the "trabeculæ," or has a secondary character as a development in the cranial wall. The compound eighth nerve (Plate VII. figs. 2, 3, 4, $_8$, and Plate VIII. figs. 2 & 3, $_8$) passes out of the skull between the postero-internal face of the ear-sac and the investing mass; it pierces the exoccipital in the adult. These latter bones present flat zygapophyses for the "atlas," which is also joined to the basioccipital, a notochordal 'buffer" remaining between the two. The "superoccipital" (Plates VII. & VIII., *s.o.*) is a massive bone; it does not, as in the "Sauropsida," receive any of the "anterior auditory canal;" and it extends halfway along the roof of the square postpituitary part of

the skull, its bony matter ending abruptly in front. So much cartilage as is here ossified belongs, indeed, to the occipital ring; but whilst ossifying the cartilage had grown forwards to join a retral growth of a similar character which had crept along the cranial ridge all the way from the ethmoid (Plate VII. figs. 3, 4, 9, 10, 11, and Plate VIII. figs. 1, 4, 5, 6). This solid, subcarinate roof to the "great fontanelle" makes the endoskeletal skull of the adult Salmon very different to that of the adult Frog ("Frog's Skull," Plate IX. fig. 6), which is barge-shaped, and has a very imperfect "deck." These two types of skull do, however, conform to each other more than would seem at a hasty glance; even in the Frog the annular ethmoid roofs in the great opening to some extent, and the superoccipital cartilage has grown to the anterior sphenoidal region. We have, moreover, in the Salmon the lateral fontanelles (*p.fo.*), as in the Frog (Plate VIII. figs. 1 & 4). The rest of the square hinder part of the cranial box is almost entirely due to the impaction into the sides of the primordial cranium of a pair of very large ear-sacs, which coalesce very early with the investing mass, and send forwards from their anterior margin a lamina of cartilage which becomes the alisphenoid, and which is separately ossified. Anticipating the account of the earlier stages, I may say that the auditory sac is enshielded by cartilage from the outside, and is never totally encased as in the Frog. Also the huge size, in the young, of the semicircular canals causes upgrowths and swellings, according to their form, in the cartilaginous shield; and more than this, for the skull of the Fish, especially behind, is related to muscular masses, hence apophyses have to grow out for their attachment and leverage.

The eye reads all this in merely looking at the end view of the skull (Plate VIII. fig. 8), which shows a curious piece of architecture, the keystone of which and the *lesser* and *greater* wings thereof are produced and snagged. Five bony buds were during the first season grafted upon each swelling ear-sac, and they have transformed those simple encasements into the angular, ridgy, and winged mass which I have portrayed in figs. 1, 2, & 8 in Plate VIII. All these, save one, can be seen from the upper surface (fig. 1); they are the "sphenotic" (*sp.o.*), the "pterotic" (*pt.o.*), the "epiotic" (*ep.*), and the "opisthotic" (*op.*): the "prootic" (*pro.*) can be seen from beneath (fig. 2), partly sliced away from the outside (fig. 3), and in transverse section (figs. 4 & 5). The inner view (Plate VII. fig. 4) and the outer (Plate VII. fig. 3, *pro.*) are most instructive as to the most constant of the periotic centres. All the figures show how massive the periotic cartilage and bone becomes, and yet the labyrinth is only very partially imbedded in the mass. I borrow from the study of a prior stage the fact that the prootic commences in the thin anterior edge of the shield behind the exit of the first division of the fifth nerve, but enclosing the second; also that the "sphenotic" begins over the ampulla of the anterior canal, the "pterotic" over the ampulla and arch of the horizontal canal, the "epiotic" over the arch of the posterior canal, and the "opisthotic" over its ampulla.

The prootics nowhere display such curious and unlooked-for characters as in the

Osseous Fish; they beguiled both CUVIER and OWEN into the supposition that they were the great wings of the sphenoid. They surround part of the fifth nerve, send their osseous matter trespassing across the "investing-mass bridge," and also down into its deep descending keels—those most ichthyic protectors of the orbital muscles (Plate VII. figs. 3 & 4, and Plate VIII. figs. 2, 4, & 5, *pro.*). A broad synchondrosis exists between the prootics and the upper bones; and below this, on the inner side (Plate VII. fig. 4), the prootic is trilobate as it embraces the hinder division of the fifth nerve (5^b) and the "portio dura" ($7''$). When the outer face of the skull has been sawn away (Plate VIII. fig. 3, *a.s.c.*, *pro.*), it can be seen that the ampulla of the anterior canal is partly imbedded in cartilage, and that the tubular communication of the ampulla with the rest of the labyrinth really burrows its substance and reenters the skull by the recess which opens outwards for the second division of the fifth nerve (5^b).

The bony bridge made by the prootics from the fore part of the investing mass articulates in front with the "basisphenoid" (Plate VII. fig. 4, *pro.*, *b.s.*), and behind with the basioccipital (*b.o.*). The two supero-external pieces carry the long concave facet for the wide head of the hyomandibular (Plate VII. fig. 3, and Plate VIII. fig. 2, *sp.o.*, *pt.o.*), and together form the "tegmen tympani," or rather its ichthyic counterpart, for here is no tympanum. The "sphenotic" is only half the size of the "pterotic," but it is a solid bone (see sections, Plate VII. fig. 11, and Plate VIII. figs. 4 & 5, *sp.o.*); it forms a strong forthstanding spur protecting the orbit, whilst the pterotic sends a similar spur backward for muscular attachment. Neither of these bones can be seen from the inner face of the skull (Plate VII. fig. 4) in a direct lateral view, nor can the "epiotic" or "opisthotic." The Bird differs from the Osseous Fish, whilst agreeing much with it, for it has all the five periotic centres; but the cartilage is not so thick as in the Fish, and it is entirely ossified; the "sphenotic" and pterotic are both small, but the former ("postfrontal") has the same shape as in the Fish and the same relation to the "alisphenoid" (see "Fowl's Skull," Plate LXXXIV. figs. 6, 8, 13, 14, *p.f.*, *a.s.*; compare especially fig. 14 with the section, fig. 4, in Plate VIII. of this paper).

In the Fish the huge sweep and vertical position of the semicircular canals makes the membranous labyrinth bear a much larger proportion to the cranial walls than in the Bird, in which the fore part of the periotic cartilage rapidly modifies itself in relation to the membranous cranium, and the anterior canal leans backwards; thus the "sphenotic" region grows out free from the labyrinth, and its ossicle looks like a mere epiphysis on the "alisphenoid." In the Bird the cerebellum excavates the cranial wall by its projecting lobe, and thus brings the little pterotic into view within; whilst the opisthotic wedges itself in between the prootic and exoccipital, and is greatly modified to encircle the mouth ("fenestra rotunda") of the small cochlea (see "Fowl's Skull," Plate LXXXV. fig. 3, *op.*, *f.r.*). The epiotic and opisthotic of the Salmon are both very backwardly placed in relation to the posterior canal (Plate VIII. figs. 1, 2, & 8, *ep.*, *op.*); they correspond in the adult Fish with their condition in the newly hatched Fowl or Chelo-

nian*, the epiotic being the larger and more conspicuous bone. Here, in the Salmon, the opisthotic has an average development for a Teleostean; but in the Cod-tribe ("Gadidæ") it is very large, and reaching down to articulate with the basioccipital, ossifies the thin protuberant cartilage that encloses the sacculus; yet in them it is quite simple and ichthyic.

Getting in front of the borrowed part of the encasements of the brain, we come in front and at the sides of the pituitary body upon parts that, without a doubt, answer to the posterior sphenoid of Man. But in the Teleostean, at best, the basal part, the "Turkish saddle," is very unfinished and the "greater wing" is very small in proportion to the "petrosal" mass; yet the "alisphenoids" are unusually large in the Salmon for a Teleostean, and it has, what many others do not possess, namely a basal bone. The extent of the posterior sphenoid is best seen when part of the skull has been sawn off (Plate VIII. fig. 3), and its general form and relation in a transverse section (Plate VIII. fig. 4); from beneath (Plate VIII. fig. 2) and within (Plate VII. fig. 4, *b.s.*, *al.s.*) it can be studied instructively. Thus it will be seen that the basal bone is Y-shaped, that it leans backwards, that it sets its foot against the end of the orbito-nasal septum, and with its arms it props up the alisphenoids. At its bifurcation it leans against the prootic floor (Plate VII. fig. 4, *b.s.*, *pro.*) behind, whilst in front of it the optic nerves (2) escape. Between the arms of this bone the pituitary body is let down behind its single leg to find no "seat" to the "saddle," save what is formed beneath by the parasphenoid (*pa.s.*): the "sella" of the Bird is very similar to this (see "Fowl's Skull," Plate LXXXII.). The "alisphenoids," although in reality forming only the second cranial sclerotome, seem as if they would close-in the skull both in the Salmon and the Bird (compare the sections, Plate VII. fig. 11, and Plate VIII. fig. 4, with "Fowl's Skull," Plate LXXXV. fig. 11). Their relations are complex, and their formation will be better understood when we come to their development; the various figures, however (Plate VII. figs. 2, 3, 4, 11, and Plate VIII. figs. 1–4), will give a tolerably good idea of their architectural relationships. These bones are not brought into relation with the "investing mass" as in warm-blooded Vertebrata, but are separated from it by the great anterior passage for the "trigeminus" (see, from within, Plate VII. fig. 4, *al.s.*, *pro.*). Looking at the inner view, we see the alisphenoid propping up the thick supracranial ridge of cartilage, articulating behind with the prootic, and in front with the orbito-sphenoid (*o.s.*), whilst it rests upon the corresponding arm of the basisphenoid. The alisphenoids bound the lateral fontanelles in front (Plate VIII. fig. 1, and Plate VII. fig. 3, *al.s.*, *p.fo.*); they are separated externally by a thick synchondrosis from the sphenotic (Plate VII. fig. 11, and Plate VIII. fig. 4), and externally (Plate VII. fig. 3, and Plate VIII. fig. 1) they clamp, as well as underprop, the great cartilaginous "culmen cranii." The alisphenoids are much more distinct from the beginning from the trabeculæ than

* They soon coalesce in the Turtle (*Chelone mydas*), and the compound bone, from its relations to the labyrinth, has been mistaken for merely an opisthotic (see HUXLEY, 'Anatomy of Vertebrated Animals,' 1871, p. 203).

the same regions in the Bird; this distinction is shown in Plate VII. fig. 4, where in front of the orbito-sphenoid bone (*o.s.*) there is seen a sinuous fissure (*e.t.f.*). This fissure had been seen and drawn by me nearly three years before its development was made out. We should soon understand all things that belong to the skull if the sphenoidal regions were intelligible; they are not, however, as yet; for have we not just seen that even the posterior sphenoid is in front of the *axial* part of the skull, and that it grows out from the auditory capsule? Not altogether, however, for the alisphenoid is continuous above with cartilage which grows backwards from the "ethmoid," the ethmoid itself being built upon the foundation laid by the "trabeculæ"—a state of things enough to suggest to us the wearing away of morphological landmarks during the ages that are past. At present I have to describe the anterior sphenoid as it exists in the adult. Neither in the Bird nor in the Teleostean Fish can any part of the anterior sphenoid be seen either from above or from below (compare Plate VII. figs. 3, 4, & 10, and Plate VIII. figs. 1 & 2, with "Fowl's Skull," Plate LXXXVII. fig. 1, *os.* 1, *os.* 2, *ps.*); in the Bird the mesoethmoid meets the prepituitary part of the basisphenoid, and in the Salmon that prepituitary part is scarcely ossified at all by the Y-shaped bone, and the coalesced trabeculæ and the keel ascending therefrom are permanently unossified. Above also (Plate VII. figs. 1, 3, 10, *o.s.*), the cartilage of the great "culmen cranii" is not infected by the bony orbito-sphenoidal laminæ.

A vertically transverse section of the coalesced orbito-sphenoids (there is no distinct presphenoid) shows well their structure, and how that they in this case, and not the ethmoid, close-in the cranial cavity. There is no "crista galli," and the perforation (Plate VII. figs. 3, 4, & 10, 1) for the "olfactory crus" is in the orbito-sphenoid. In the vertical section we see the twin bone grafted upon the "culmen cranii" above, and upon the thick swelling partition that grows upward from the shelving trabeculæ below. This double bone has metamorphosed some cartilage, but, like the Y-shaped basisphenoid, it is principally membranous; in the Sturgeon the orbito-sphenoids do not graft themselves upon the cartilage, and in the Fowl the two pairs of these bones have no orbito-sphenoidal cartilage to graft themselves upon (see "Fowl's Skull," Plate LXXXVI. fig. 11, *os.* 1, *os.* 2).

Foundation, side-walls, and roof,—all these are *facial* in the ethmoidal or nasal region: we are in front of the skull now, and the brain which did overtop and overhang every thing else in the head, and was, indeed, the largest thing there, is now relatively a retired series of small lobes and bands (compare Plate VII. fig. 4, showing the cranial cavity, with Plate I. fig. 8, showing a sectional view of the head in my earliest stage), so that the ethmoidal region can now be studied in an extracranial manner; we need not try to torture it into the vanguard of the vertebræ, or even into a "cranial sclerotome."

Save in expansion and size, the "trabeculæ" have undergone but little alteration in their under surface since the time of hatching, and even two or three days before; but above they have been subject to great change, by means of the various outgrowths that have sprung from them (Plate VIII. figs. 1 & 2, *tr.*). Looking at the bare skull

from beneath, we see two symmetrical cartilaginous slabs, totally unossified, which together form a rough kind of cross deeply grooved along the mid line, for it has its equal moieties bevelled towards the middle. These moieties were formed of the flat tape-like trabeculæ, which met each other at an obtuse angle, so as to present a ridge towards the overlying membranous cranium. They were bowed out far beyond the boundary of the pituitary body, and by the end of each bowed part they coalesced with the corresponding moiety of the investing mass; now, however, there is no such connexion, the trabeculæ *are again free*, and they end by two small points with a rounded emargination between (Plate VIII. fig. 2, *tr.*). Each free point is the termination of a lanceolate convexity, and these convexities diverge in front, terminating on the outer edge of the trabeculæ. These facets have relation to the underlying "parasphenoid;" for here the flat part (Plate VII. fig. 2, *pa.s.*) becomes carinate above, and also gives off the "basitemporal alæ." But these facets have another meaning than their relation to the parasphenoid; for they are the first budding (arrested, indeed, and functionless) of the "anterior pterygoid processes" (see "Ostrich's Skull," Plate VII. fig. 4, *a.p.*, and "Fowl's Skull," Plate LXXXIV. fig. 11, *a.p.*). These processes are the "basipterygoids" of Huxley (see Proc. Zool. Soc. 1867, p. 418). Another pair of facets are formed beneath the arms of the *cross*; these are for junction with corresponding facets on the palatal bar; at these points the trabecular skull-base becomes greatly expanded. Corresponding with what I have said in my account of the development of the Frog's Skull, I call these outstanding parts, that tend to make the facial arches into a kind of basketwork, like the gill-crate of the Lamprey, the "facial connective growths." Those by which the palato-pterygoids join the trabecular bars appear during my rather long "first stage;" but those which foreshadow the second pair of connectives in the "Sauropsida" cannot be seen until the metamorphic changes are well nigh over.

Having sent out the "palatal connectives" the trabeculæ gradually contract: the part in front of the palatal connectives may be called the "cornua trabeculæ;" between those projections we have the transverse partition formed between the eyes and nose-sacs, whilst the further continuation of the trabeculæ is modified in relation to the nasal organs. The broad part immediately in front of the facets is the floor of the nasal sacs, and corresponds to the "subnasal lamina" of the Frog ("Frog's Skull," Plate VII. fig. 6, *s.n.l.*). Below, this is traversed by a curved ridge, which grows towards its fellow, anteriorly, in an elegant lyriform manner; the two do not meet at the mid line, but in front of them the thick short trabecular horns unite their substance, have a groove between them, and end in a bevelled facet; each "horn" is separated from its fellow at the end by a rounded emargination. Moreover, each horn has at its tip a pair of short, thick upper labial cartilages ($u.l.^a$, $u.l.^b$), the inner of which is the largest; they are joined by fibrous tissue, but they have a joint cavity between themselves and the "horns." Between the nasal sacs the trabeculæ are badly soldered together; in front the cartilage loses its substance in places, which becomes replaced by fat; further back, however, there is a large, apparently meaningless, cavity, filled also with fat. Below, between the

converging arcuate ridges, a large canal is seen, occluded in its middle by the largest of four or five swellings of cartilage, that thus clumsily, as it were, have resoldered the trabeculæ together. Looking at the upper view (Plate VIII. fig. 1, *al.s.*), we see feeble attempts at the formation of "aliethmoidal" and "aliseptal" laminæ; but the "septum nasi" only exists as the clubby coalesced "trabecular horns." Above, the cartilage near the mid line is imperfect; then, behind that, we see a piece of the "lamina perpendicularis" (*p.e.*) crop up to the surface, and behind this the opening which is the anterior remainder of the "great fontanelle," overhung by the free fore end of the "culmen cranii." This remnant of the "fontanelle," and the vacuity a little in front of it, both open into the great mesoethmoidal fat-cavity (Plate VII. fig. 4, *m.n.c.*). Is there any morphological meaning in this fat-cavity, and in these deficient solderings of the "trabeculæ cranii" in front of the cranial cavity?

If the reader will refer to the fourth Plate in JOH. MÜLLER'S magnificent work on the Myxinoids ('Vergleichende Anatomie der Myxinoiden'), he will be able to answer this question for himself; meantime I will refer him to the sectional views of this Salmonine remnant of the azygous nasal sac of the Myxinoid with its "Nasenöffnung" above and its "Nasengaumenöffnung" below (see Plate VII. figs. 4, 7, & 8, *m.n.c.*).

The facets for the palatines are not on the widest part of the ethmoidal region; for, above, the huge "ectoethmoidal" wings form both wall and roof to the orbit in front, and, largely ossified, they form the so-called "prefrontals" (Plate VIII. figs. 1 & 2, and Plate VII. figs. 1, 2, 3, & 9, *l.e.*). These elegant shelving ethmoidal wings are separated above by a notch from the "mesoethmoidal" region, which has at that part become the "culmen cranii." Exactly between these antorbital expansions the "mesoethmoid" is, as has just been stated, occupied by fat, but further backwards it reappears a veritable "lamina perpendicularis" (Plate VII. figs. 4 & 9, *p.e.*). Outside the fat-cavity the antorbital wall is pierced by the "olfactory crus" (1); in the lateral view (Plate VII. fig. 3, 1) this can be seen emerging from the orbito-sphenoid behind, and reappearing in front of the "ectoethmoid" in the recess for the "nose-capsule." The ridge above this recess is the rudiment of the "aliethmoid" of the Bird and other high types, and the ridge below is the edge of the "subnasal lamina" of the Frog.

If the reader will refer to my paper "On the Fowl's Skull" (Plate LXXXVI. figs. 8 & 9), he will see that the "prefrontal" bone answers to the region called "pars plana," the seat of the "middle turbinal," whilst the upper unossified part of the lamina is the counterpart of the foundation for the "upper turbinals." Of course there can be no "inferior turbinal," as there is no specialized "septum nasi" from which it could grow as an outgrowth from an "aliseptal lamina."

The Fowl gives voice as to the meaning of the "culmen cranii;" I had described the retral continuation of the ethmoid along the mid line, above the olfactory groove, as the "crista galli," but corrected this error (see "Fowl's Skull," note to p. 762, and Plate LXXXI. figs. 3, 4, & 5, *eth.*). If this elegant roof had continued its growth backwards in the Fowl instead of degenerating into a spike, we should have had what does appear in the

Salmon's skull; I am, of course, supposing an equivalent growth from the "superoccipital." When we come to the earlier stages of these parts the meaning of what is here written will become much plainer, and the reader will do well to keep the adult condition of the various parts always before him whilst studying their incipient stages.

With regard to the next arch, the "pterygo-palatine," I must confess that the state of things in the Frog made me hesitate in classing this arch with the rest as a morphological equal. It certainly has a sluggish development even in the Osseous Fish, where it attains to its fullest growth and is for a time entirely distinct; moreover it only acquires the typical sigmoid form of the facial arches just as it is losing its distinctness from the first postoral bar. This arch is but little developed in the Urodeles, and scarcely chondrifies at all in the Sauropsida and Mammalia. Yet my figure of it in the Chick ("Fowl's Skull," Plate LXXXI. *pa.*, *pg.*) is perfectly correct, and my early stages of the Salmon will show a marvellous amount of harmony between the "Teleostean" Fish and the "Carinate" Bird in this and in many other parts.

To put the matter clear at once with regard to the Frog, let me repeat what I have described in that creature—namely, that at first there is no pterygo-palatine arch whatever; that it is fairly suppressed during the whole of the proper ichthyic or larval period, only existing as a feeble "secondary connective;" that when the tail is disappearing and the lungs developing it only has reached to the condition of the Lamprey; and, finally, that it never becomes distinct, either from the trabecula in front or from the mandibular pier behind. I am somewhat inclined to attribute the feeble and slow development of the second preoral arch in the Salmon to the prepotent growth of the eyeball; yet that will not account for its suppression in the Frog, where the eyeball is relatively much smaller (see "Frog's Skull," Plate IV. fig. 1, and Plate V. fig. 1).

When the investing parosteal bones are removed from the facial arches of the Salmon we have what is displayed in Plate VI. fig. 2, and Plate VIII. fig. 9. Let an imaginary line be drawn through the substance of the cartilage that separates the "mesopterygoid" and pterygoid (*m.pg.*, *pg.*) in front from the metapterygoid and quadrate (*mt.pg.*, *q.*) behind: such a line will pass through a knob of cartilage above; this is where the "orbitar" process of the mandibular arch has coalesced with the inturned or hooked upper (=posterior) end of the pterygo-palatine rod, and the line drawn will show the whole extent of the coalescence. These parts do not coalesce in the "Abranchiate Vertebrata." The dentigerous bony palatine does not wholly ossify the palatal region of the bar, a large knob articulates with the maxillary near the end of the prepalatal spur; the "ethmo-palatal," an earlier process, tied to the trabecular facet by strong fibres, does not ossify, and the postpalatal portion has a soft core. The "mesopterygoid" (*m.pg.*) overhangs the outer side (Plate VI. fig. 2), but is large, convex below, inturned, then concave, and then flat behind, on the inner side (Plate VIII. fig. 9). This flat posterior portion overlaps the pterygoid (*pg.*), which clamps the lower edge of the bar behind, is most developed on the inner side, and, like the "mesopterygoid," overlaps the inner face of the quadrate bone. Here there is no "os transversum" or "ecto-

pterygoid," and the *innermost*, or submesial pterygoid, is much larger than the pterygoid, the counterpart of the "internal pterygoid plate" of Anthropotomy. In Fishes this bone is very constant from the Ganoid Sturgeon to the Teleostean Perch; I have never seen it in the Amphibia, and as yet only in *Anguis fragilis* amongst the Reptilia; it has only failed my search in the Ostriches and Fowls amongst the Birds, and I am satisfied that it is not uncommon in the Mammalia.

In the ordinary language of embryologists the mandibular arch is called the first facial, for the palato-pterygoid is mostly reckoned as a rudiment growing out from the mandibular rod above, whilst the "trabeculæ" had all along, until Professor HUXLEY showed their true nature, been regarded as processes growing forwards from the "investing mass." In my description of the Frog's skull the mandibles are, on account of the suppressed and non-separate condition of the palatals, classified as the second facial arch; in this memoir the mandibles will be considered as the third arch, but the series must be divided into the "preorals" and "postorals." In all Teleosteans, and in some to a most extreme degree, the gape of the mouth is placed at a great distance from the head. In such Fishes as the Dory (*Zeus*), in *Epibulus*, in *Fistularia*, and in the "Hippocampoids," there is found the extreme of Teleostean modification of the mouth; but in the most moderate degree of specialization, as in the Salmon, the hinge of the jaw is carried away from the head, first, by a double condition of the quadrate, and, secondly, by the descent of the top of the pier away from the side of the head and its attachment some distance down to the overgrown pier of the next arch (Plate VI. fig. 2, Plate VIII. fig. 9). All this modification shows that the Teleosteans are Vertebrates specialized to the uttermost for their own kind of life, and that they are indeed one of the culminating branches of the vertebrate *Life-tree*; hence, I think, arises the wonderful harmony, in many respects, between their structure and that of the branches and twigs of another "leader" in this genealogical tree: I refer to the Bird.

The top of the mandibular pier, "metapterygoid" (*mt.pg.*), is not let down so far in the Salmon as in the more typical Teleosteans, where it is commonly on a level, at its top, with the attachment of the "stylo-hyal;" it passes halfway down, and both it and the succeeding pier being broad, it largely overlaps its successor. The whole pier is oblong, the upper bone, "metapterygoid," being squarish with produced angles, the lower, the "quadrate," triangular, with a free grooved posterior wing, and at its inverted apex a condyloid facet.

Observe that the synchondrosis between these bones rises in front of the upper piece into a boss, and swells out behind it into a knee; the boss is a primordial lobe; the "orbitar process" lies in front of the eye in the long horizontal mandibular pier of the Tadpole (see "Frog's Skull," Plate v. figs. 1 & 3, *or.p.*); the "*knee*" is the retention of the original curve of the facial arch, which I shall afterwards describe. All in a row are these *knees* or bends in the postoral arches; that on the trabeculæ has been lost, and the curved part of the pterygo-palatine arch has coalesced with the orbitar process of the mandibular pier. On the inner side (Plate VIII. fig. 9, *qu.*) the quadrate is grooved,

between its broad part and the periosteal wing, to receive a peg from the next pier, and by this elegant carpentry the two piers are strongly coupled to each other.

The free part of the mandibular arch is one third longer than the pier; it is strongly clamped by a bone which is grafted upon it, most on the outer side; this is the articulare.

The "coronoid process" is part of this bone, and not due to the Meckelian rod; but the hooked process behind the angular process is due to the character of the original segmentation of the terminal piece. The "articulare" is snagged, ribbed, and splintered, and only ossifies the proximal part of the mandible, the rest being a strong, rounded, gradually tapering rod (Plate VIII. fig. 9, *ar.*, *mk.*).

As in the Bird there is no "mento-meckelian" bone, such as occurs in Frogs and Man. No morphologist has ever been more richly repaid for his labours than he who traced the metamorphosis of the second "postoral" in the Frog; equal pleasure and profit has attended the unveiling of the mystery of the Teleostean hyoid arch. This arch has its fullest development, if not its highest metamorphosis, in the Osseous Fish. On each side of this huge *swing* there are seven bones and four broken-up segments of cartilage, besides an azygous pier, which has its own bony plate, besides, in the Salmon, thirty-three parosteal bones. *How* all this has been made out of a single pair of facial rods let embryology declare. Not now, however; at present let it be assumed that the second "postoral" does cleave a long cleft down its substance, that the foremost larger part stays atop, and that the narrower part slides slowly but surely down to the *knee* on the synchondrosis of the foremost piece. The great factor in the swinging-power of the Fish's mouth is the uppermost part of the larger anterior division of the arch. At first hooked beneath the fore part of the auditory capsule, it keeps under a ledge formed by the bulging of the horizontal canal, and then the hinder piece having escaped downwards out of its way, it grows along nearly to the extreme end of the sac.

The long scooped facet for this element, the "hyo-mandibular," is shown in lower and side views of the skull (Plate VII. figs. 2 & 3, and Plate VIII. fig. 2). Below the unossified, long, convex condyle of the hyo-mandibular there is a knob for the cup on the opercular (*op.c.*); below this the bone gradually narrows and stops short above the knee like bend; then comes a broad cartilaginous tract, and below that the ossified "symplectic" peg (*sy.*), which turns forwards to fit into the groove of the quadrate. On the inner and posterior face of the out-bowed synchondrosis there is a small rod of largely ossified cartilage, this is the "stylo-hyal;" it is the *secondary* suspensorium of the second narrower division of the second "postoral," and is attached by ligament to a cup above and to a cup below; there is evidently a small joint-cavity above within the ligament, but not below (Plate VIII. fig. 9, *st.h.*). I do not find this "stylo-hyal" (Cuv.) until I come to the fourth stage, and it has no separate representative in the Frog; yet in Fishes it is found from the lower "Ganoids" (the Sturgeons for instance) up through all the higher osseous kinds; not, however, in "Myxinoids," nor "Plagiostomes," which are represented by very early conditions of the Teleosteans.

This dropped semi-arch, thus suspended, is very large, and carries the infero-internal gill-cover fold, the branchiostegal membrane with its many parosteal rays. The main arch has an arcuate outline within, is flat above and knobbed below; but this knobbed part, from the Sturgeon upwards, is segmented off, is cupped to fit to the convex end from which it has been taken, but there is no joint-cavity; this distal part has two bony centres, and the upper third of the main arch has a centre distant from the rest of the bar. From above downwards "epihyal," "ceratohyal," and hypohyal; these may be the names, for the distal piece answers to the "hypobranchials," and not to their azygous keystone; it has its own keystone, the "glossal," or rather "basihyal," a thick flattened bar, covered at top, sides, and end with a dentigerous ectosteal plate (Plate VI. fig. 1, and Plate VIII. fig. 9, *ep.h.*, *c.hy.*, *h.hy.*, *g.h.*). These huge "cornua" are strongly tied to the sides of the basal piece, near its end, and the first "basibranchial" runs up to the converging bars (Plate VIII. fig. 9, *b.br.*).

The smaller arches, much smaller *from the first* in this high type, are devoted to respiration, all save the last, and are seen from their inner side (Plate VIII. fig. 9, *br.*); they are a regular series, decreasing, however, in size and specialization from before backwards; they pass below within the hyoid arch, as it passes within the mandibular, telescopically. Each bar is normally segmented transversely into four cartilages, conjoined by a strong, short, fibrous ligament, and each of these has its own ectosteal sheath. The fourth arch has its upper piece unossified, and wants the distal segment; the fifth is still more aborted, having a small separate upper cartilage and a larger lower piece which is ossified; this arch is dentigerous and abranchiate, and is called the "inferior pharyngeal." The normal arches have their segments called "pharyngo-," "epi-," "cerato-," and "hypobranchial," and the keystone pieces are the basibranchials; there is only one for the fourth and fifth arches, and it is unossified and segmented from the bar in front; the three foremost have coalesced. These arches tend to fork above; the first segment sends off a sort of pedate process (Plate VIII. fig. 9, *p.br.*), the next has its upper segment bifurcate, and also the next, the third articulates with the fourth and sends a fork from its "epibranchial" segment, the fourth sends out an epibranchial lobe, somewhat 3-lobed itself, and the fifth is simple. The third basibranchial (Plate VIII. fig. 9, *b.br.* $_3$) is clamped on each side by a descending process of the corresponding "hypobranchial," and it sends downwards a cartilaginous hook from its lower end; these are for muscular attachment.

First Stage.—Salmon-embryos, before hatching, with the facial arches simple.

With such specimens before him as those from which the following descriptions have been taken, it is not a little difficult for the worker to keep himself from wandering into general Embryology.

This snare will, however, be avoided as much as possible, reference to the general bearing and relation of parts being made just enough to make the matter clear to the reader. As an introduction to this starting-ground, the inquirer will do well to read the

latest and best abstract of what is known as yet of the development of the Vertebrata; this is given in Professor HUXLEY'S new work entitled "A Manual of the Anatomy of the Vertebrated Animals" (see pp. 3–13).

In the younger embryos which formed the subjects for my *first stage*, the "primitive groove" had not closed over the cephalic (Plate I. figs. 2, 4, 5) nor over the caudal extremity of the long tape-like germ.

At present the rudiments of the nose, eyes, and ears are very imperfect, the olfactory sacs are merely (Plate I. fig. 1, *ol.*) pits surrounded by a circular ridge of the "epiblast," the folds of the eyeball (*e.*) are not coalesced, and the auditory involutions (figs. 1, 3, 6, 9, *au.*) are still widely open.

The peripheral portions of the "blastoderm" extending over the yelk form a bag so wide open above that its rim reaches to within a short distance of the posterior margin of the mouth, close behind the converging MECKEL'S cartilages (Plate I. fig. 1, *u.v.*, *mn.*). In this early stage all the principal parts of the head have their rudiments differentiated; but these rudiments lie in the midst of a very soft stroma, and much care has to be taken in hardening and even colouring the specimens before the various organs can be made out. The most immature embryos worked out by me are illustrated by figs. 1 & 2, Plate I.; and although the parts which have begun to form the skull and face are *coloured* as though they were cartilaginous, yet their actual condition was merely that of more consistent tissue than that in which they were imbedded. This tissue was indeed composed of the "mother-cells," very small, of hyaline cartilage; and it could easily be seen, in the case of the facial arches, that the apparent *rods* were merely *tubes* composed of finely granular matter, lying in and also enclosing a thoroughly diffluent tissue. As to *degree* of development, the first two pairs behind the mouth were the rods most distinct, next to them the branchial-arch rudiments, then the trabeculæ, and lastly the "subocular" bands, the rudiments of the pterygo-palatine arch.

My illustrations will appear to the reader as representing strangely twisted, *oblique* objects; they are true to Nature, however, in that the upper and lower planes of the head, in the unhatched Salmon, are placed in such an oblique manner that only one *eye-dot* appears when the eggs are examined with a pocket lens (see Plate I. fig. 4, the head seen from above). Hence all bird's-eye views of the head, whether upper (fig. 2) or lower (fig. 1), are strangely unsymmetrical; and it is useless at present to seek in these imprisoned young for either the swelling cerebral vesicles, with which the embryologist is so familiar, or for that very important tilting-over of the fore part of the brain, causing the "mesocephalic flexure."

The flat edge of the down-kept membranous cranium is seen from below like a second superciliary ridge (Plate I. fig. 1). One eyeball, it may be indifferently either *right* or *left*, is fully seen below, whilst the other is mainly seen above, and only peeps down to the lower plane. So large are the ear- and eye-sacs that they overlap each other; this is seen in specimens that have suffered no compression. Most of the structures with which I have to deal are formed in what I would call *secondary strata* of the "meso-

blast," enfolded very largely in their differentiation by involutions, *tuckings-in*, of the "epiblast;" these are mainly on the under surface of the head, which now just projects free of the yelk mass. This *subcranial* mass of tissue becomes *thickened* in certain directions, *puckered* into more distinct ridges and furrows, and *cloven* into bands or rods, the epiblast freely growing into every available cleft, and giving additional separateness to the mesoblastic structures. Hence, in the cephalic part of the embryo, the so-called mucous membrane, that of the mouth and fauces, is not a hypoblastic production, but is formed by ingrowths of the "epiblast" down to the point where the true mucous membrane begins; the lining of the mouth and fauces should be rather called "inner skin" than "mucous membrane." By means of the peculiar thickenings and puckerings of that part of the blastoderm which underlies the projecting head, we get an *upper* and a *lower* palatal region; in the higher Vertebrata, the Crocodilia and the Mammals generally, a third and lowest palatal floor is formed by a peculiar infolding of the *supraoral* strata.

The uppermost and also *innermost* "palatal bands" ('Gaumenleisten,' MÜLLER, see his 'Myxinoids,' pl. 4) are formed out of a delicate tract of "mesoblast" immediately underlying the membranous cranium, under the rudiment of the first vesicle (Plate I. figs. 1 & 8, *v.* 1, *tr.*); they are invested below by a tract of "epiblast," the primordial mouth-roof, which is made and *exposed* by the puckerings of the "blastoderm." These are in reality the first facial arch; their relation to the rest of the series is seen in a sectional view (Plate I. fig. 8, *v.* 1, *tr.*); the huge eyeball and the dipping-in of the tissues to form the mouth-cavity makes their relation to the rest of the series difficult to understand. RATHKE, who regarded these bands as continuations of the "basilar plate" or "investing mass of the notochord," called them the "rafters of the cranium," *trabeculæ cranii*. Their morphology is much more easy to be understood in the embryo of the Frog; whilst the mouth is hard to interpret in that type, and comparatively easy, as it appears to me, in the Salmon. A much smaller object than a rafter would have served better as a comparison for those rods which stand in the van of the facial phalanx, namely a pair of *curved forceps* (see Plate I. figs. 1 & 2, *tr.*). That these bands belong to the same series as the rest of the facial arches, and that they are formed out of the same structure of the "blastoderm," is evident if we examine them in the Frog (see "Frog's Skull," Plate III. fig. 3, 1, *tr.*, and Plate IV. fig. 1, 1, *tr.*), where they are the largest of a series gradually decreasing in size backwards. Moreover, in the second stage of the Frog's skull (Plate IV. fig. 1), when the trabecular rods have acquired the curve inwards above which is peculiar to the series, then they are really subocular rods, for they lie in the very substance of the outside of the cheek, and curve round under the eye, there being at that time no pterygo-palatine arch in their way. But the Salmon-embryo at its earliest differentiation of organs shows itself to belong to a new and higher dispensation; in its earliest infancy it bears the impress of a nobler type. The blades of these tiny forceps are perfectly simple in form, they are not riveted anteriorly (=below); this anterior part has neither the second lobe nor the outward turn, which makes them

lyriform afterwards; the blades pass round the pituitary body, to which they are as nearly related at the beginning as they are in the Frog in my third stage (*op. cit.* Plate IV. fig. 9, *tr.*). There is no clear distinction at present between that layer of epiblast which forms the skin and that which invests the rudiments of the brain as the primordial or membranous cranium. Hence the position of the trabeculæ (see Plate I. fig. 8, *tr.*) is between the epiblastic cerebral tube (imperfectly closed) and the palatal skin (*enderon*), and they are formed out of and enclosed in that thin tract of "mesoblast" which becomes differentiated not only into these trabeculæ, but also into the membranous cranium*.

There is a great difference in the embryos at this early stage; for while some have their mouth gaping and the angle of the mandible drawn back, others (see fig. 3) have a peculiar likeness to their *sire*, the old male Salmon, the rudiments of the lower jaw being very long and strongly hooked upwards; these, however, are best for a contemplation of the morphological nature of the mouth. The mouth of the Frog-embryo caused me so much trouble that I almost despaired of classifying it (*op. cit.* p. 145, and note), but now I seem to "feel the light" from this translucent embryo. Looking at my third figure, and considering that the foremost arch is wrapped up in the succeeding folds of the face, then the *seriality* of the converging bars and intervening furrows will be understood.

The facial clefts formed by dehiscence of the thinned interspaces of the rib-like thickenings of the face are not formed at the same time; the first cleft, which I have discovered between the first and second *preorals*, does not become thoroughly distinct until after hatching. The first *post*oral cleft is now visible (fig. 3), but *it* has lagged behind the second, for the cleft *in front* of the mandibular bar was formed first.

That cleft is not one of a pair like the rest, but is double, and forms an azygous V-shaped opening, bounded in front by the second preoral, and behind by the first postoral bar; this is the mouth (m). The palatines are primordial structures as distinct, even now, as the eyeballs which rest upon them; they bound the opening gape above, and reach in front to the nasal sac, and behind to the auditory capsule, overlapping there the remarkable superorbital band (*s.ob.*). Now, in conformity with their long suppression and late appearance in the Frog, even here in the Salmon their differentiation into hyaline cartilage is very tardy; in my fourth stage the rod will be seen to enclose a protoplasmic pith, and in the fifth their apex will have melted into the fore edge of the next arch behind†.

The section (Plate I. fig. 8, m) will show what space is forming for the mouth and

* In the longitudinal section (Plate I. fig. 8) the trabecula (*tr.*) is coloured, as though it were *showing through* the palatal skin, for it could not be shown in a section of the skin, being at a little distance from the exact mid line; the same is partly true of the next bar, pterygo-palatine, but the rest are made naked at their very ends.

† Here let me warn the reader against relying on terms of mere local relation, such as *pre*frontal, *post*frontal, and the like: the term *sub*ocular is good for immediate use in description; but at first the trabecula is the "subocular" in the Frog-embryo; then in the Tadpole (compare "Frog's Skull," Plate IV. fig. 1, *tr.*, with Plate V. fig. 1) it is the mandibular pier (1st *post*oral) which is the subocular bar; here, in the Salmon, the subocular bar is the rudiment of the "pterygo-palatine arcade." We must not rest until our knowledge is put upon a sound *morphological basis.*

fauces between the infoldings and thickenings that have formed beneath the brain. The pituitary body (*py.*) lies between and almost *upon* the converging mandibular rod ($v._3$), and these terminate above in a transverse line a little behind the pointed end of the notochord (*nc.*). An equal space exists in front of the pituitary body, between it, behind, and in the membranous cranium and subocular bar in front: there is no space between the trabecula and the cranial sac; it cleaves fast to the skull from the first.

Several minor stages and various conditions of the mandibular arch (third facial, first postoral) are given; perhaps the most important is my very earliest (Plate I. fig. 1, $v._3$). Here it is but a granular tube filled with and enclosing fluid stroma, and yet it has three most important regions marked out. The first of these is the slender "metapterygoid" band, running up and curving inwards as far as the next arch: this part has its normal position under the fore edge of the auditory capsule.

The next region is the middle, the swelling part, which shows the commencement of the "orbitar process," here, at the beginning, having a position which it only acquires in the fifth or metamorphic stage of the Frog (see "Frog's Skull," Plate V. fig. 1, and Plate VII. fig. 1, *or.p.*). The third region is the *Meckelian*; it becomes afterwards a free segment, the mandible; it is clubbed at its end as in the Tadpole, but it lies as yet some distance from its fellow. In more advanced embryos (Plate I. figs. 3, 7, 9, $v._3$) the first postoral has grown very much; it is very variable as to length, even at exactly corresponding stages, and the clubbed Meckelian end has spread into a flat spatulate expansion (Plate I. fig. 7, and Plate II. fig. 1, *mn.*). This bar is not dissected out in figs. 3, 6, & 9, but in fig. 7 we see its uttermost development as a simple tape-like band of cartilage, its flat apex and "orbitar process" turned inwards beneath the front of the auditory sac, and its Meckelian region converging to its fellow in front, and flattening out at the symphysis. The apex, with its "orbitar" expansion is well shown with its relation both to eye- and ear-ball in fig. 5 ($v._3$, *mn.*).

The first clear differencing and formation of the second postoral (hyoid) is shown in fig. 1 ($v._4$); it has an enlarged and incurved apex, and is thickened in the middle and below: the umbilical vesicle (*u.v.*) reaches the mid line between the two bars. This condition lasts but a short time; for in embryos but a little more advanced (figs. 3, 7, 8, 9) the part of the blastoderm enclosing the yelk has retired so as to expose the under surface of the lingual region, and even the opercular fold of the second postoral bar; moreover the ear-sac (*au.*) has still its great lipped opening. Now, but not before, the first postoral cleft (fig. 3, $cl._3$) is very distinct, and the top of the long hyoidean band of cartilage largely curls itself under the auditory sac (figs. 3, 5, 7, 10, $v._4$, *au*). Also we now find the first of a series of azygous cartilages, which are denied to the three front arches; this is the "glosso-hyal" or true "basihyal" piece (figs. 7, 8, *g.h.*). But, further, the first two postorals would be remarkably alike, save that the apex of the second is broader and more developed even now than that of the first, so early does each arch show the marks of its hereditary modification. As all the arches have a tendency to project forward, this keystone piece stands mostly in front of the lateral bars; it will be

seen to be the same with those that succeed. These arches are formed in that part of the blastoderm which lies within the huge opening of the "umbilical vesicle;" that vesicle attaches the fore part of its neck, at present, to the under surface of the rudimentary tongue, with its enclosed "basihyal" cartilage (Plate I. figs. 3 & 8, *u.v.*, *g.h.*, *v.* 4), and because of the heart (*h.*), which is situate in the mid line, these bars are wide apart at present. There are five pairs of rods behind the hyoid arch; these become the branchial arches (*br.*), all save the last pair, which become dentigerous and are always feeble; they all suffer from the general non-symmetry of the head, are all smaller than those in front of them, but all except the last early acquire the elegant sigmoid in-hooked form. That these Salmon-embryos rapidly assume the more highly specialized characters of a noble "Teleostean" Fish, and are much further from the lower "Myxinoid" types than the Frog-embryo, is evident if we compare my very earliest condition (Plate I. figs. 1 & 2) with the counterpart stage in the Frog ("Frog's Skull," Plate III. fig. 3).

That part of the primordial skull of the Salmon which is *quasi-vertebral* (its "peri-notochordal" region) is very small, and forms the floor for the "medulla oblongata" (Plate I. figs. 2 & 8, and Plate II. fig. 2, *nc.*, *i.v.*). Of all the facial arches the trabeculæ come nearest to the investing mass in this type (Plate I. figs. 2 & 5); whilst in the Frog (*op. cit.* Plate III. figs. 4–6) they are the furthest from it. In a number of specimens I was able to make out, most clearly, the free truncated ends of the moieties of the "investing mass" or "basilar plate" (Plate I. figs. 2 & 3, and Plate II. figs. 4 & 5, *iv.*).

The abrupt manner in which this "*præ*-protovertebral" tract ends in front is quite remarkable; it is as square as though it were really one of the proto-vertebræ, the foremost*.

In my most immature specimen (Plate I. figs. 1 & 2), studied as a transparency, but in the upper view (fig. 2), having the skull-floor partly laid bare from above, the twisted condition of the embryo gives the notochord and its investment a turn toward the left side; it is seen to reach the trabeculæ; but its investing moieties (*iv.*) quite run short, so that there is a peculiar and sudden abortion of the primordial vertebral structure. All that is built upon this foundation is the occipital arch and the "prootic bridge," and the mansion of the brain is built up from many a source foreign to these mere axial rudiments.

There is a skull-rudiment which develops in a manner unexpected by me; this is the

* I can now throw a little more light upon the Fowl's skull than when I wrote upon it. Professor Huxley gives a figure of the primordial skull of the Fowl in his 'Elements' (p. 138, fig. 57, F^1), and reproduces it in his 'Manual' (p. 18), which agrees very closely with my first stage (Plate LXXXI. fig. 2). In these figures the "trabeculæ" converge towards each other over the ends of the investing mass, and this mass terminates in a truncated manner on each side, the *squared end* looking *forwards* and outwards; the two structures are not seen, however, as distinct. In my next stage (Plate LXXXI. fig. 8) the blades of the trabecular *forceps* have opened out, and the investing mass is now mesiad of the apices of the trabeculæ, which are plainly seen. Not so plainly seen, however, as in the third stage (Plate LXXXII. figs. 1, 2, 3, *lg.*), where these apices have become long, free, rounded rods, with a cellular interior, such as I find in the trabeculæ of the embryo of the Boa, *Eunectes murinus*.

primary "superorbital bar" (Plate I. figs. 1, 2, 3, 4, 6, 7, *s.ob.*); it is much more than the seat of that frequent additional bone which overshades the eye in Fishes; in the fifth stage I shall describe the cartilage which develops in it as a boundary to the "great fontanelle."

The auditory sac is only partially invested with cartilage, and at this stage it is an irregular and fenestrate shield (figs. 2 & 5, *au.*), imperfect within, above, and below (Plate I. figs. 2 & 5, and Plate II. figs. 2 & 4). As far as I can see from various views, the great blastodermic involution which forms the ear-sac shuts off the labyrinth before the outer opening begins to close, although this gaping space itself is very temporary. The sac itself seems to be formed from the epiblastic layer, which has developed a roof to the labyrinth over the rudiments of the three semicircular canals, thus shutting off the new sense-organ from the outer skin and its primordial opening. But the mesoblastic layer has developed immediately around the new *racemose labyrinth* (Plate I. figs. 2 & 5) a partial investment of young cartilage; this cartilage has not crossed over below the primary opening, nor has it finished the floor (see Second Stage, Plate II. fig. 4), a deficiency being left there for several months; nor does it ever in this Telostean wall-in the labyrinth, craniad. The finishing of the upper and lower faces of the periotic cartilage is remarkable and instructive; and whilst the primordial opening of the sac is closing-in the semicircular canals are getting more roof, which grows from before backwards, and which is not completed in newly hatched fry (see Fourth Stage, Plate III. fig. 6, *ep.*). No such gradual or even *partial* growth of cartilage is seen in the Frog; in that type the epiderm, *at least*, is closed over the sac before hatching, when the head and tail of the embryo *pitch* very little beyond the yelk-mass. Then, indeed, there is a primordial "fenestra ovalis" ("Frog's Skull," Plate III. fig. 3, and Plate IV. fig. 1), but otherwise the cartilaginous ball is complete, except where it allows the "portio mollis" to enter on the opposite side. Soon (that is in Tadpoles less than half an inch in length) this fenestra is filled in, again to reopen by the segmentation out of its own substance of a *stopper*, the "stapes" (*op. cit.* Plate IV. fig. 7, and Plate V. figs. 1, 2, & 4).

We shall see the last of the primordial fenestra ovalis of the Salmon in the seventh, or first summer stage, but I have already shown that there is no reopening.

The auditory cartilage is entirely free at first, but as my first stage is passing into the second it coalesces with the "investing mass" by two connective bands that enclose the primordial "fenestra ovalis" (Plate II. figs. 2 & 4); this takes place a little before the fusion of the trabeculæ with the same plates. The foregoing description will be now supplemented, and in some degree recapitulated, by a description of the transverse sections. Two of these sections (Plate I. fig. 10, and Plate II. fig. 1) are made through the eye-balls, and two through the ear-sacs (Plate I. fig. 11, and Plate II. fig. 2). The first of these sections (Plate I. fig. 10) is of a very immature but unusually symmetrical embryo, one answering to figs. 1, 2, & 8 as to development. At this part the "umbilical vesicle" (*u.v.*) is quite free from the projecting head of the embryo; a clear watery space intervenes between the two parts, and this space is larger on each side of the flat head. Two

principal strata of the blastoderm are seen above this space, and between them another shallow transverse vacuity, the mouth.

The anterior cerebral vesicle (*c.* 1) is full of a gelatinous fluid, but its more condensed peripheral part is very soft and of no great extent; it is somewhat grooved below. Below this shallow sulcus, in the tissue between the membranous cranium and palatal skin, there are seen the sections of two chondrifying bands, and in the sulcus between the eye and brain a thickening of a triangular form is observable; this is softer still. The inner pair are the trabeculæ in section, and the outer the subocular or palato-pterygoid bars. In the thin "hammock," with its thickened middle part, which is swung at a small distance below the space of the mouth-cavity, there is a more solid but flat pair of sections; these are the outspread ends (see also fig. 7, *mn.*) of the first postoral rods, their symphysial ends. So that we have here, beneath the first cerebral vesicle:—1st, a capsule; 2nd, a layer of "mesoblast," containing the cartilaginous rudiments of the first and second præorals; 3rd, a layer of enderon (palatal); 4th, below the oral cavity two layers of epiblast and one of mesoblast, this latter containing the first postorals or third facial arches. A section from the same part in a more advanced embryo, or near to the second stage, shows a great change (Plate II. fig. 1); here the section, which is through the very middle of the exposed and hidden eyeballs, is also posterior to the "prosencephalon" and through the middle of the "thalamencephalon;" their imprisonment has strangely hindered their symmetrical growth, but they have acquired much substance; we are here *behind* the cavity of the prosencephalon, and in front of the next, and therefore in the most solid part of the brain. The left half of the "thalamencephalon," like the left eye and the left half of the "hemispheres," is smaller than the right. The more solid tissue of the first, second, and third arches is shown in section, and the flattened Meckelian region is well displayed at the symphysis of the chin. A glance at this figure and the last, for comparison's sake, will show how fast the differentiation of layers has taken place; but that which is of most importance to notice is that a new cavity has been formed, the "anterior palatal recess" (*a.p.r.*). This marked splitting-up of the facial strata divides the mouth from the layer in which the trabeculæ and subocular rods are imbedded, and is well seen in older embryos as a recess between the upper (trabecular) palate and the "naso-frontal process" (see Fourth Stage, Plate II. fig. 10, *n.f.p.*, *a.p.r.*).

The next section (Plate I. fig. 11) is through the fore part of the *right* ear-sac, but the obliquity of the head makes even this *true* transverse section miss the *left*; it is in front of it, and also of the notochord. In this stage the eye- and ear-balls overlap each other, and hence a section which barely escapes the eye takes off the fore part of the ear. The brain is here somewhat more developed than in figs. 8 & 10; but the razor passed through the more solid cerebral substance which lies immediately behind the thalamencephalon, in front of the pituitary body, and across the overhanging fore edge of the "mesencephalon." The razor missed the "subocular" boss on both sides, whilst the trabeculæ, the mandibular bars, and the *right* hyoid were cut through *obliquely*. On the

left side the umbilical vesicle is free, but on the right it is continuous with the blastoderm beneath the hyoid bar. At this point three things are clearly seen—the fore face of the auditory sac is chondrified, its outer part being pitted by the anterior canal, the hyoid bar has crept beneath this region, and the "primordial auditory involution" lies over the supero-external region of the sac; it is here cut through its middle. If this be compared with the other figures, especially figs. 2, 3, & 6, it will be seen that the naked upper part of the labyrinth lies just within the primordial opening in the skin. Hence I infer that the "labyrinth" itself has been constructed out of that layer which was primarily uppermost, the "epiblast," and that the next layer within, the "mesoblast," may be credited with the formation of the cartilaginous shield.

The last of these sections (Plate II. fig. 2) belongs to the very close of the first stage, and is much in advance of the last; it is also from a point further back, although the broad hyoidean band has been displayed. Here the "epencephalic" region is cut through, the third vesicle, and the medulla oblongata; the apex of the notochord and of the "basilar plate" and the fore part of the "labyrinth" with its "shield" are severed; these parts have now coalesced beneath the rudimentary "sacculus." This band is a "connective" passing in front of the "inferior fenestra" (fig. 4, *fs.o.*); it is very thin. On account of the natural obliquity of the parts, the first and second branchials are shown with their basal piece; they are prematurely distinct in this specimen; for I find them less specialized in others, which in other respects are more advanced*. The hinder part of the mouth here must still be "epiblastic" as to its lining, for it is in free communication, by the visceral clefts, with the outer skin.

Second Stage.—Unhatched Salmon with hyoid arch splitting up.

Notwithstanding the fundamental identity of the morphological plan of growth in Vertebrate embros, the detail is marvellously varied, and these variations take place very early; both the *precocity* and the *amount* of these variations, especially as seen in this and my former subject, the Frog, have surprised me again and again. The light obtained from *that* has indeed been useful for *this*; yet not as a clear, flooding light, but merely as a lantern to my first steps.

Therefore this piece of research has been made with a greater sense of comfort and confidence, but not with less caution and care. The manner in which the second postoral arch is, as it were, chopped and split into fragments is very unlike what I have described in the Tadpole; and more, it gives as yet little promise of becoming a "Teleostean" hyoid apparatus. The three foremost arches have not changed much, they are quite unsegmented; but the second "postoral" (Plate II. fig. 3), besides having its foreturned lower extremity cut off and rounded into a globular submesial joint, has been

* The reader may think that I have drawn a little upon my imagination for the deep yelk-bed in which the auditory region is made to lie in this figure, and for the awkward manner in which the chorion is made to compress the young cerebellum; all I can say is that the actual object, uninjured in relation, although shaven through, appeared as strange to me.

cleft from apex to base into a broad anterior and a narrow posterior band. The round distal piece belongs rather to the extremity of the former than to that of the latter; thus the front division is connected with the azygous "lingual" or "basihyal" piece by this distal segment, the "hypohyal." It is useless looking to the Tadpole for an explanation of this; and as we shall soon arrive at a "Ganoid" stage, we may do well to look among the "Plagiostomes"—that is, we must search a lower morphological level.

In the Brazilian Torpedo (*Narcine*)* there are two bars in this region, the foremost, however, being slender and the other broad (see Müller's 'Myxinoids,' pl. 5. figs. 3 & 4, *a.d.*). In my last paper (p. 195) I ventured to call the foremost bar a "metapterygoid," much wondering why it rested upon the broad hyoid suspensorium. I retract; it is quite *behind* the mandibular region, and the two together are surely the split-up second postoral, the anterior a feeble "hyo-mandibular," and the posterior a massive "ceratohyal;" there is no "hypohyal," as far as I know, until we get to the "Ganoid" Sturgeon.

In the higher groups we have long been pestered with two cartilaginous and bony tracts on each side in the substance of the second postoral arch; hence the misunderstanding of the relations of the "incus;" this element may now be said to be safely fixed in its own place as the "antero-superior segment" of the split-up hyoid arch, and the mammalian representative of the Fish's "hyo-mandibular."

The "basihyal" (Plate II. fig. 3, *gh.*) has now become a thick lozenge-shaped mass of cartilage, strongly wedged between the "hypohyals." This preparation, which has been flattened out for display, shows considerable modification in the form of the mandibular bars; they are more strongly sigmoid, and the "orbitar process," above the abrupt bend, is very distinct; its most definite reappearance is in Chelonians and Birds. The thick "subocular" flap is acquiring a more solid palato-pterygoid pith; towards it, in front, the still small and distinct trabeculæ (*tr.*) are sending a small connective lobe, the first rudiment of the "ectoethmoid" with its "superpalatal" facet. The same stage is illustrated by the figure of an *uncompressed* specimen (Plate II. fig. 4), from which the postoral part of the face has been removed to display the auditory sacs from below. The oldest specimen of the first stage (Plate II. fig. 2) may illustrate this, which is but little older; here (fig. 4) the "notochord" is twisted to the left side and projects beyond the ear-shaped flaps that form the end of the "investing mass." Behind, these moieties contract, first suddenly and then gradually, growing to a point as they form the "basioccipital" region. The primordial "fenestra ovalis" notches both the prootic cartilage and the investing mass, and with the help of the two secondary isthmuses a very elegant circular window is left; not through it, but a little externally, the otolith may be seen shining through the cartilage. The anterior, horizontal, and posterior canals have bulged out the cartilage in their respective regions; above, there is still a fenestra over the posterior canal; this is not closed for some time to come (see next stage, fig. 7, *ep.*). Between the investing mass and the ear-sac in front there is a deep notch; into this the trabecular apex is creeping. Another head at this stage has supplied me

* Professor Gegenbaur in the recently published third part of his 'Untersuchungen.'

with the most lucid appearance of the relation of the investing mass to the trabeculæ. These translucent Salmon-embryos show their parts with intense clearness, and here especially a definite image is important. This individual had broader trabeculæ (fig. 5, *tr.*) and investing mass with narrower ends than others examined; the knee-shaped trabecular apices, bent before the pituitary body was within shot-range of them, turned inwards, and lay crosswise *upon* the free ends of the investing mass, overlapping them unconformably.

The blades of these minute "forceps" evidently move, opening as they grow, and bring themselves into conformity to and into coalescence with the ends of the investing mass; this will be seen in the next stage.

Third Stage.—Unhatched Salmon with MECKEL'S *cartilages free.*

This stage does not yield in interest to the last, and the growth now must be very rapid, the metamorphic changes taking place as fast as the development of flowers in spring time.

I think it is very probable that the third stage is the morphological equivalent of that which is persistent in the Rays, just as in the unhatched *chick* we come upon "Rhynchosaurian," Struthiine, and Tinamine stages, as we delve from above downwards into the more simple and unspecialized conditions of the embryo Fowl. Certainly I shall soon come to a most evident "Polypterine" stage. Standing on the level of those depressed outspread "Elasmobranchs," the Rays, we see what fitnesses for aquatic life may arise in organisms halfway between the simplest possible conditions of a Fish and the noblest spiny-finned "Percoids." If these flat-headed, flat-bodied, long-tailed, broad-flippered Salmon-embryos had grown largely without *zoological improvement*, to the Plagiostomes they must have gone, no other place would have been found for them *.

One of the first preparations made by me of the Salmon-embryos was that which is figured in Plate II. figs. 6 & 7. This preparation of the primordial skull was very exquisite, but showed such strange characters that it had to wait for some weeks for interpretation; the second stage, just described, was the *sine quâ non* for that. Articulated to the fore and under part of the well-developed periotic capsule, I found *two* similar, nearly equal, strong cartilaginous rods, each growing athwart, under the head, and only directed slightly forwards. The foremost was *too far back* for it to be the mandibular pier, and they both were too well developed, too large, and too far forwards and outwards to answer to the first and second branchials. Thus in a few moments I was able to reason out what they were not; the missing link (my second stage, fig. 3) turning up, it soon became evident what they were. Yet this temporary conversion of the second "postoral" into a "double couple" of arches disturbed the complacent manner in which I was making the subdivision of the Tadpole's facial parts into a measure for the rest; the structures seen in that type are not the most perfect, but are low in kind, and therefore cannot be

* Those of my earliest stage, in which the non-symmetry is at its least degree (Plate I. fig. 10, *transverse section*), have the Raiine type of head in perfection.

used as a rule. Yet this lesson was learned from the Frog—namely, that part of an arch being segmented off from the primary bar may *travel up* or *travel down* just where the specializing force pleases; the "hyoid cornu" of the Frog travels up, that of the Osseous Fish travels down. The anterior division of the second postoral in the Salmon now stands forwards and touches the first postoral arch (*hm.*, *q.*); it has left its own distal segment, the "hypohyal" (*h.hy.*), to the hinder moiety, which moiety is still articulated like the fore piece, by a flattened hook, to the ear-capsule; the "basihyal," or *tongue piece* (*g.h.*), still keeps its relation as the keystone, and still projects forwards considerably.

But that which marks this stage is the segmented condition of the first "postoral" or mandibular arch (compare Plate II. fig. 3 with figs. 6 & 7). In this simple morphological process my former subject failed for interpretation; *there*, in the Tadpole, the *pier* is of extreme length, so long as to carry the "orbitar process" in front of the eye; but the free Meckelian arch is for some time very small indeed (*op. cit.* Plate III. fig. 12, and Plate IV. figs. 7 & 8, *mk.*); and although it *acquires* the sigmoid bend and the "angular" hook, yet at the first it is a mere *bud* pinched off, as it were, from the lower end of the bar, which before segmentation (*op. cit.* Plate III. fig. 3, and Plate IV. fig. 1, 2, *mn.*) is strongly inturned below. Here there is something very *chirurgical* in the way in which this segment is "cut out without hands," the invisible knife passing now across, now along, and then dexterously slanting through, so that a *ball* is formed on the upper part, and a *cup* and a long rounded angular process on the lower. This specimen is of the *short-jawed* variety (compare Plate I. figs. 1 & 3), and MECKEL'S cartilages pass athwart and then curve backwards, perfectly *Ray-like*. Already the pier of the mandibular arch is escaping downwards from its original position, and has grown very little since the last stage, and, in this specimen at least, the orbitar process is less marked. If the position of this pair of cartilages be considered, it will be seen that they well illustrate the so-called palatal cartilages ("Gaumenknorpel") of *Narcine* (MÜLLER, *op. cit.* plate 5. figs. 3 & 4, *e*) and the azygous palatal cartilage ("unpaariger Gaumenknorpel") of the Sturgeon (*op. cit.* plate 9. figs. 10 & 11, *b*). It is the *top part*, the inturned outspread apex of the arch, which is segmented off in *Narcine* on each side; in *Acipenser* it is evident that these segments early coalesced to form the "azygous metapterygoid"*. It is perfectly normal that the facial arches should *turn in* and flatten out at their apex; those the least specialized, the gill-arches, constantly do this, and the substitution for gill-papillæ of small teeth is a very gentle change and superaddition of function. Certainly the foremost arches are subject to most modification; but even the outbowing of the trabeculæ is perfectly normal, and their hooked apices only enclose the pituitary body because of its contiguity; the hooking was a morphological fact before any such relation was brought about by specializing growth. As to the segmentation of the mandibular arch in *Narcine* and *Acipenser*, let the reader compare their metapterygoid segment, just referred to in MÜLLER'S work, with his plate of the *Chimæra's* skull (*op. cit.* plate 5. fig. 2, *qqq*), and see how in that type the "pharyngo-branchials" are segmented off to form outspread, smooth, arched roof-plates to the pharynx; thus the order, harmony, and *simplicity*

* See 'Monthly Microscopical Journal,' June 1873, plate 20. figs. 1, 2, 5, *mt.pg.*

of the whole matter will appear to him. As to the languid, feeble, tardy-growing "subocular" bands, these are not really chondrified in this the third stage; they are, however, larger. But the trabeculæ have grown immensely (Plate II. figs. 6 & 7, *tr.*). Looking at them in this stage, before they have done more in relation to the cranium than to marry themselves to the "investing mass," we shall see how facial arches must be modified that have to grow in a directly horizontal manner, adapting their apex to some convenient fastening-point behind. Save in the lack of segmentation of the out-bowed part, these trabeculæ at this stage are very exactly like the next pair (the palato-pterygoids) of the Pelecanidæ, of *Sula* and *Phalacrocorax* at present, and of *Pelecanus* itself, as soon as they have combined and sent upwards a common crest; the divergence of the pterygoids in these and other Birds is the true morphological equivalent of the divergence of the trabecular apices outside the pituitary space.

We have seen already that the trabeculæ at a very early stage (Plate I. fig. 5, *tr.*) have their leafy ends bilobate; the outer lobe is the first morphological germ of the "ethmo-palatine;" it, in reality, is a conjugational "stolon" from the minute trabecular stem. Already, in a very few days, the trabeculæ have grown tenfold; they have also articulated, as facial arches are wont to articulate, with their successor bars; and now we have the junction of the ascending part of the palatine with the "lateral ethmoid," never to be seen wanting again in our long ascent to Man. Underneath (fig. 6, *tr.*) the ethmoidal region is transversely ribbed: these *ribs* grow out afterwards as the pedicles (the serial counterparts of the "basipterygoid processes"), to which the palatines are suspended. In front the other lobe meets its fellow; it is thick, and the two diverge at a large angle; they together form the rudiments of the nasal septum and the "subnasal laminæ." Above (fig. 7, *tr.*) the "ectoethmoidal" wall is quite soft; it separates the nose from the eye: the whole of the cerebral roof is also quite uncartilaginous.

The original membranous space below the primordial ear-opening is now a small fenestra over the posterior semicircular canal (fig. 7, *ep.*); the "fenestra" in the periotic floor (fig. 6, *f.s.o*) is less; moreover, the whole capsule, now well united to the investing mass, has developed considerably since the last stage. Now the occipital arch (*b.o.*, *e.o.*) can be seen behind the auditory capsules; but the two divisions have not united above; they are nearer, however, than the figure (7) would indicate, as it is a little outspread for display.

The branchial arches do not grow at the same rate in different individuals; they are more differentiated in the oldest of my first stage (Plate II. fig. 2, *br.*) than in those examined in this, the third. Here (Plate II. fig. 8) these elegant blunt hooks have coalesced by their lower straight end, and the coalesced part is turned backwards, swollen, and half cut off as a median piece. This is similar to what I found in the formation of the sternum in the embryo ox ('Shoulder-girdle and Sternum,' plate xxix. fig. 1), where the median piece is made out of the ends of the lateral pieces. In the hyoid arch of the Salmon (Plate I. fig. 7, *g.h.*) the median piece is truly and *primarily* azygous; here, in the branchial arches, it is a *secondary* azygous element, made up of the coalescing ends of a pair of rods. As yet there is no basal piece behind the third

arch. There is now no appearance, nor will there be for several days to come, of any further subdivision of the branchial arches; their respiratory papillæ are beginning at this stage as *dermal* growths. With the "primitive groove" filled in, with considerable consistency of the brain, and with the skeletal growths so far advanced, the young Salmon is becoming too active and strong for further imprisonment.

Fourth Stage.—Salmon-fry in the act of hatching and newly hatched.

The figures given are from young Salmon with the head only protruding from the shell (Plate II. figs. 9 & 10, and Plate III. figs. 1–3), and of others which had enjoyed a day or two of freedom (Plate II. fig. 11, and Plate III. figs. 4–6). The expansion of the cerebral vesicles is a correlate of that peculiar bend downwards of the fore part of the head which is called the "mesocephalic flexure." Now, for the first time, the head assumes the form so familiar to the embryologist in the air-breathing Vertebrata. This overbending of the cerebral vesicles evidently is not the *vera causa* of the arrest of the notochord behind the smaller, dipping vesicle, the pituitary body, but is a correlate of the sudden finish of the investing mass: a cause for both these arrests has yet to be found. This, which may possibly be a modification taking place during long secular periods, is also correlated with the small amount of independence seen in the cartilaginous cranium, which, where it is not largely aborted by the implantation of the ear-bulbs, yet grows over the membranous cranium from any neighbouring cartilaginous tract. I said *grows over*, that is in the lower types; but the most important part of the nervous system is largely roofed in simply by investing bones. As yet, in this fourth stage, the only part of the membranous cranium floored or surrounded by cartilage is the "medulla oblongata." A sectional view, both during hatching (Plate III. fig. 3) and after (fig. 5), shows the form of the principal parts of the brain, and the relation of its parts to *axial* and facial structures. The earlier specimen (fig. 3), even, has now budded out a well-defined "prosencephalon" ($C\,1^b$), the more solid "thalamencephalon" ($C\,1^a$) lying on a pair of balks, which are the bent and flattened trabeculæ (*tr.*): the pituitary body (*py.*) has no "rest," but lies between the trabecular hooks, amidst gelatinous blastema. Even the fore part of the "medulla oblongata" (*m.ob.*) rests upon a fold of the primordial enclosing membrane, which retires to line the back of the pituitary body; this is where Rathke placed his "median, or azygous trabecula," evidently a mere membranous band projecting beyond the notochord in the mid line, and having no morphological relation to the trabeculæ proper: even these parts were misunderstood by this most excellent embryologist. If these sections be compared with the earliest stage (Plate I. fig. 8, *nc.*), a notable difference will be seen—namely, that the pointed end of the notochord has retired somewhat, and that the apex of its sheath has grown downwards behind the pituitary body as a free tongue-like process.

In these sectional views we see how the walls of the face are broken into ridges and furrows; and in fig. 5 especially the relation of both the præorals is shown—the second (subocular) forming the upper cheek-wall, and the first (the trabecular) forming a

curved beam on which the first vesicle rests. The trabeculæ end in and fill the cavity of the "naso-frontal process," which ends below and behind in a free lip—the *floor* of the "anterior palatal recess" (see also Plate II. fig. 10, *a.p.r.*). In the section of the more advanced specimen the "subocular" (pterygo-palatine) rod is brought into view; between it and the trabeculæ there is seen the bulging orbital floor (see also Plate II. fig. 10, and Plate III. fig. 2, *or.*). Here, under the eyeball (see also Plate III. fig. 4, *l.cl.*), is a *cleft*, which I find very distinct, and which Professor HUXLEY shows me is the "lacrymal cleft;" it is the true *first cleft*; the oral opening is the second, and therefore the tympano-Eustachian, or first postoral, is the third. This cleft is also important as stamping the true visceral-arch character upon the two præorals. When arches can be shown me which combine the characters of *ribs* and *visceral arches*, then I will treat of them as morphological *varieties*; *species* they are, to all intents and purposes, being altogether independent of the *perineural* axis—most largely developed when furthest in front of it, and excluding the heart instead of containing it. The trabeculæ at the time of hatching are solid, so also are the first and second postorals; but the chondrification of the pterygo-palatine and branchial arches is tardy, and they still contain a central cavity filled only with protoplasm (see Plate II. fig. 10, *p.pg.*, and Plate III. fig. 3, *br.*). Morphologically, we are now at the level of the "Chondrosteous Ganoids;" a familiar example, happily extant, is the Sturgeon. Now in the life-history of this Teleostean we for the first time see the "stylo-hyal," and the Sturgeon, standing above the Plagiostomes and below the higher Ganoids, shows it for the first time, zoologically. Even in the second stage the Salmon has gone beyond the Plagiostomes in having segmented off a "hypohyal; in this it agrees with the Sturgeon, which, however, has its own specialization in the complete subdivision of the first half of the second postoral, the "hyo-mandibular." Even at the time of hatching, the first postoral cleft is being obliterated, but the cutis being removed, it can be seen as an opening undergoing division into *two*: the lower of these is the tympano-Eustachian, and is entirely occluded by the symplectic; the upper part remains open in most Plagiostomes and Ganoids as the "spiracle." The amount of metamorphosis which takes place before the fry has fairly escaped from the egg is evident (see Plate III. figs. 1 & 2); for almost all the essential characters of the Teleostean face have already appeared. The most remarkable of these are the low position of the first postoral (*mt.pg.*, *q.*), the equally low position of the posterior division of the second postoral (*c.h.*), the appearance of the little connecting segment (*st. h.*), and the development of the *halved hook* of this, the hyoid arch, into the backwardly turned massive head of the "hyo-mandibular" (*h.m.*). Moreover the individual segments have not only gained their new relationships, they have also acquired very nearly their permanent form; for the muscular masses are now developed, which have their origins and insertions in harmony with the nature of this type of Fish.

The huge eyeballs still obscure the morphology of the upper part of the face, and their sockets especially, at present over large (see Plate II. fig. 10, and Plate III. fig. 2, *or.*), widely sever the pterygo-palatines and their *cleft* from the trabeculæ.

The former (*p.pg*) are still distinct from the quadrate (*q.*) with its projecting "orbitar process;" the "metapterygoid process" is blunt and short, and has not the flattened shape it afterwards assumes. The "hypohyal" has now well applied its hollow upper end to the rounded base of the "cerato-hyal" (*c.h.*), and the "basihyal" is seen to be the first of a series of azygous cartilages, which serve to all but the last abortive branchial as key-stones. The ascending and lessening branchial arches are becoming stout, and are developing their respiratory papillæ and their alternating *cogs* that convert the gill-arches into a *colander*.

A bird's-eye view of the primordial skull of a recently hatched Salmon (Plate III. fig. 6) shows the advances just spoken of as having been made since the third stage. Even now, over the posterior canal, the cartilage is deficient; the fenestra is a remnant of the great space beneath the primary infolding of the "blastoderm."

Fifth Stage.—Salmon-fry of the second week after hatching.

This stage does not yield in interest to any going before or after it; taking it for all in all the skull has now the most perfect parallelism with that of the culminating "Ganoids," such, for instance, as the *Polypterus*. In that light I have seen it, and know not well how to describe it otherwise than by using a running comparison with what is seen in that fine waif of the seas of the primary epoch. Two of our chief experts in the "Ganoidei," namely Professors Huxley and Traquair, are of one mind with me in this view: they both see the Ganoid type in this plane of the Salmon's *ascending* growth, and thus there are three witnesses to attest to the truth of the matter.

If the reader would follow me in the details of this stage, he should keep open before him Dr. Traquair's "Cranial Osteology of the *Polypterus*" (Journ. of Anat. and Phys. vol. v. pl. 6). In this condition of the Salmon's skull there are no ossifications of the cartilage; the great *first bone*, the parasphenoid, has appeared, and, as in the lower Ganoids, is of huge relative size; it reaches from between the nasal sacs to beneath and behind the auditory (see it in dotted outline in Plate IV. fig. 3, in longitudinal section fig. 4, and in transverse section fig. 7, *pa.s.*). The "supraethmoidal plate" (fig. 4, *eth.*) has appeared as a fine film of bone in the thickness of the subcutaneous stroma, and the frontals (Plate III. fig. 9, *f.*) are styloid ossifications, forming eaves to the low cranial roof. The thickened stroma below the trabecular cornua is not ossified into the "vomer;" several, however, of the parosteal and ectosteal tracts of the face are already present, and will soon be described. What I have to draw the attention to principally, is the greatly altered state of the primordial (cartilaginous) cranium; the ossifications are of secondary importance. A comparison of the skull as it existed a week before (Plate III. fig. 6, *upper view*) will show the *rate* and the *degree* of metamorphic change which has to be contemplated now.

Even now the membranous cranium is growing upward, free of the fore face substructure; the whole of the inflated brain-sac, very large in relative size, as yet, may be studied in its own morphological independence. The trabeculæ, stretched forward under

it, like the arms of a swimmer, have already coalesced, and send their outspread palms beneath the nasal sacs, to which they form a floor, as well as serving in this complex building the purpose of beams to the brain-chamber and rafters to the palate*.

Nothing, perhaps, in the whole Vertebrate morphology has such a vegetative freedom of growth into branch-like and leafy outgrowths, spreading outwards and reaching far forwards, as the first facial arch. Yet it is upon the trabecular modifications that the very *facies* of the types largely depends; the Shark, the Sawfish, the Skate, the Tortoise and the Bird, the Whale, and even Man himself, all these largely owe their "prognathism" or their "orthognathism" to arrest or extension of the trabecular growths. Here, as in the *Polypterus* (TRAQUAIR, *op. cit.* plate 6. figs. 2 & 3), the muzzle is broad and depressed, owing to the great outgrowth of the early two-leaved end of each trabecula. *Upon* the coalesced "cornua" (Plate IV. fig. 2) there has arisen an elegant X-shaped rudiment of the median ethmoid and nasal septum in one. Between the hinder legs of the X is seen an opening (shown also *from behind* in Plate III. fig. 7); this deficient fusion of the two sides thus preserves the counterpart of the Lamprey's nasal opening (MÜLLER, *op. cit.* plate 4). On each side of the median upgrowth we see the "subnasal lamina" (figs. 1–3, *s.n.l.*), on each side of the snout the divided "upper labials," and outside the ethmoid the articulation of the palato-pterygoids (*p.pg.*). The X-shaped "mesoethmoid" (ossified in *Polypterus*, see TRAQUAIR, figs. 1–3, *E*) is continuous with the shelving, inturned "ectoethmoid" (Plate III. figs. 7 & 8, *l.e.* 1); these growths, hard to be understood, are continuous below with the pedicle for the palatal facet (Plate IV. figs. 1–3, and Plate III. fig. 7). Where the olfactory crura escape in front to ramify on the nasal sacs (Plate III. fig. 8, 1), there the ectoethmoid can be seen to be continuous, below, with the outspread "trabecular cornua" ("subnasal laminæ"), and above to have a mutual bond in the *new* cranial roof over the "prosencephalon" ($C\ 1^b$). In the transverse section through the nasal sacs (Plate III. fig. 7, *ol.*) the commencement of the sloping roof is, of necessity, cut through obliquely; but its structure and meaning cannot be misunderstood if it be looked at in the *dissected* and *bisected* skull (Plate IV. figs. 1–4). This elegant roof has no *side walls* to support it; it is, as it were, thrown like a *tarpaulin* over the brain-sac (see also Plate III. fig. 9), and is tied by cartilaginous ropes, behind, to the walls of the ear-chamber. Where this structure is cut through at its convergence in front (Plate III. fig. 8) we have a *cincture* of cartilage (see Dr. TRAQUAIR's remarks, *op. cit.* pp. 170, 171), similar to that which is seen in the Frog ("Frog's Skull," Plate VII. fig. 9).

This ethmoidal "tentorium" contracts and thickens to form the part which in the adult

* We must be very cautious of interpreting *continuity* of even cartilaginous structure as necessarily indicating morphological simplicity. Here, in the Salmon, the cranium is free from the trabeculæ as it is not in other types. We must keep also an expectant watch for the solution which may turn up of the *after division* of the skull-segments and ear-organs of the Mammalia; in that class there seems to be a reversion to even a Myxinoid type of structure, for the nasal sacs, growing backwards under the skull, divide the trabecular base from the proper cranial floor.

I have termed "culmen cranii;" *then* it stretches backwards as far as to the occipital cincture; *now* it covers only the first and part of the second cerebral division (Plate IV. figs. 1 & 4). The "great fontanelle," which in the adult is covered in and reduced to two small lateral rudiments over the postsphenoidal region, is now a most elegant heart-shaped and large space (Plate IV. fig. 2, *fo.*), through which, in the dissected skull, half the basal region can be seen. Even in the adult Frog ("Frog's Skull," Plate IX. fig. 6, *fo.*) there is as much open space, for it reaches further forwards, although more covered in behind. If it be well considered, this expanded fontanelle of the young Salmon is essentially like that of the adult *Polypterus* (TRAQUAIR, *op. cit.* plate 6. fig. 2), which is bounded by a limiting cartilage that runs behind into the postfrontal part of the ear-sac; this cartilage is like a *wall-plate* which has had part of the roof removed from it above, and part of the wall taken from beneath it. The creeping backwards of the ethmoidal "tentorium" at the mid line causes the emargination in front of the fontanelle; and each "funis tentorii" is continuous behind with the sharp cartilaginous crest that arises as an upgrowth from the auditory sac, subparallel with the elegant curve of the "anterior semicircular canal." Reference to the profile view of the skull (Plate IV. fig. 1) will satisfy us that we have in this peculiar band the cartilaginous pith of that remarkable "supraorbital bar," which I have described in the first stage (Plate I. figs. 1, 2, 3, 4, 6, 7, *s.ob.*), which stretches from the nasal to the auditory sac. On account of their origin in the early embryo they may be called the "supraorbital bands" (*s.ob.*); they have no distinct counterpart in the Frog or Fowl, but the retral part of the roof has a very evident counterpart (see "Fowl's Skull," Plate LXXXIII. figs. 2, 4, 5, *growing backwards from eth.*). But the roof-cartilage is well developed in Birds generally; in the "*Struthionidæ*" it is ossified separately from the "pars perpendicularis" ("Ostrich Skull," Plate VIII. figs. 3 & 10, *eth. p.e.*), whilst in the Cassowary (ibid. Plate XIV.) it is enormously developed, and becomes the well-known "helmet." I need scarcely mention the free roof-growth in Sharks, both ordinary and "Chimæroid," and also in the Sturgeon.

Returning to the "trabeculæ," we find that they gradually narrow backwards towards the pointed apex of the cordiform pituitary space; they thicken as they become narrow, and elbow out strongly before they apply themselves to the upper surface of the now rounded apices of the investing mass, from which they were very distinct in the specimen figured.

The pituitary body is let down through the cranial floor (Plate IV. figs. 2–4, *py.*) on to the subcutaneous parasphenoid; but it occupies very little of the open space, which is further enlarged by free communication with the "posterior basicranial fontanelle" (RATHKE), the gap in which the apex of the notochord lies. To this latter space the orbital muscles (figs. 2 & 3, *o.m.*) converge and lie (see Plate V. fig. 1, *o.m.*) upon the parasphenoid; at present there is no "prootic bridge" covering them above; the apex of the notochord lies upon their "raphe." The "investing mass" (*i.v.*) is now largely confluent with the auditory masses; in front each moiety is separated from the prootic region by a rounded notch, and behind each side is developed into two lips; those below

become the basioccipital articular ring, and those above the zygapophyses for the first cervical vertebra. Sectional views (Plate III. fig. 11, *behind*, and Plate V. fig. 5, in *front*) show the increasing thickness of the basilar plate from before backward. The lateral and superior parts of the occipital cincture are everywhere continuous with the related parts of the periotic capsules (Plate IV. figs. 1 & 2): these structures are peculiarly elegant at this stage, as the cartilage only thinly veils the curves and swellings of the membranous labyrinth, which, like the brain (fig. 4), is now very large relatively. The apertures for the hinder division of the fifth nerve (the front division escapes over the notch), the "portio dura" of the compound seventh, and the "vagus" and its companion, these can be seen piercing the periotic walls (figs. 1–3, 5^b, 7^a, 8). Above (figs. 1 & 2) a gentle sulcus separates the growing roof from the elevation caused by the anterior and posterior canals; the latter, swelling out behind, form the "epiotic" eminences. The most projecting part laterally is formed by the horizontal canal, and under it (fig. 3) is the ridge, which sets bounds externally to the facet for the extended head of the hyo-mandibular (figs. 1 & 3, *h.m.*). In the middle of the under surface the skull-base is swollen into an oval eminence on each side, and the cartilaginous part of this swelling is deficient outwardly; here still lingers the primordial "fenestra ovalis;" and mesiad of this the cartilage is very thin (Plate V. fig. 5), for here is the "sacculus" with its "otoliths." In front the auditory sac grows into a laminar form, and this thin edge gradually narrows as it passes above into the "supraorbital band;" this ingrowing lamina becoming much more developed forwards, gives rise to the "alisphenoid," which is distinct neither from the band above nor from the ear-sac behind; it is some distance from the investing mass. There is at present no rudiment of even the very rudimentary "basisphenoid" of the adult. The whole of the "anterior sphenoidal region" is membranous at this stage (Plate IV. fig. 7, *o.s.*). A description of the sectional views, although involving some recapitulation, will serve to make the description clearer. A longitudinal section (Plate IV. fig. 4) shows that the roof-cartilage growing back from the ethmoid only lies over the fore part of the "mesencephalon" (C^2); anteriorly the "mesoethmoid" ends abruptly over the nasal sacs; over this part the thin "superethmoidal" lamina of bone (*eth.*) is seen. The nasal sac (*ol.*) lies upon the "trabecular cornu," and to it the olfactory crus (1) is passing; it pierces the antorbital wall. In front of the trabecular horn the "premaxillary" (*p.x.*) is cut through. The trabecular floor (*tr.*) is continued to beneath the "thalamencephalon" (C 1^a) and then diverges: the pituitary body (*py.*) is seen in front of the notochord (*nc.*). Beneath the trabecula is seen the thin parasphenoid (*pa.s.*), but not the "vomer;" this antecedence of the former bone brings this stage to a level in this respect with *Lepidosiren*. Part of the "cerebellum" (C 3) is covered with cartilage, the "superoccipital" (*s.o.*); the medulla oblongata (*m.ob.*) lies on the notochord. But the "prosencephalon" does not lie upon the trabecular floor; it rests upon the wings of an "interorbital septum" (*i.o.s.*), which is at present entirely membranous. A more enlarged view of the middle of this section (Plate IV. fig. 5) below shows the orbital muscles passing beneath the notochord on each side of

the pituitary body (*o.m.*, *py.*, *nc.*); this lobe does not yet reach the parasphenoid. A section like the fore part of the last (fig. 6), but to the right of the mid line, shows the opening of the nasal sac (*ol.*), the inner face of the eyeball (*e.*); the "ectoethmoidal," or antorbital wall, is cut through external to the roof, and is seen articulating with the palato-pterygoid bar (*p.pg.*), in front of which is the principal upper labial (*u.l.*"); the premaxillary (*p.x.*) is cut through, and the upper jaw is seen from the inner side. The first and second transverse sections (Plate III. figs. 7 & 8) have already been spoken of; in the latter the forks of the parasphenoid (*pa.s.*) are cut through, and in the first it is severed in the vomerine region. In the third section (Plate III. fig. 9) the "prosencephalic" lobes are cut through; and this part of the membranous cranium is roofed over by the ethmoidal "tentorium," the free edges of which are bound down by the styloid "frontal" (*f.*). The cranial walls pass down into the "interorbital septum" (*i.o.s.*), which is continuous below with the perichondrium of the tilted and coalesced "trabeculæ" (*tr.*). The parasphenoid here is arched and outspread laterally, in accordance with the lower surface of the trabecular floor. The huge eyeballs (*e.*) are separated by copious gelatinous tissue, keeping the olfactory crura (1) from the septum, which is here at its highest. The fourth section (Plate IV. fig. 7) is through the "thalamencephalon" (C 1") and the fore part of the "mesencephalon" (C 2), on each side of which the *tent-ropes* ("superorbital bands") (*s.ob.*) have been severed behind the rudimentary frontals; as this section is through the eye behind the entrance of the optic nerve and in front of their exit from the cranium, they are seen in section here (2) near the lowered interorbital septa. The trabecular floor is flatter here, and so also is the parasphenoid which underlies it (*tr. pa.s.*). The fifth section (Plate III. fig. 10) is very instructive also; it is through the middle of the "mesencephalon" (C 2), the fore part of the pituitary body (*py.*), the most diverged and terete part of the trabeculæ (*tr.*), the back of the orbit (*or.*), and cuts through that part of the "superorbital band" (*s.ob.*) which is passing insensibly into the auditory sac, its "sphenotic" region; a downward growth from this part of the cartilaginous skull gives rise to the "alisphenoid." The exquisite infoldings of the parasphenoid (*pa.s.*) are here seen in relation to the pituitary body, exactly between the elbowed trabeculæ (*tr.*). The sixth section (Plate V. fig. 5) has been already partly described; it exposes the arch of the anterior and the ampulla of the horizontal semicircular canals, the "utriculus" and the "sacculus;" it shows the deficiency of the cranial roof at this place over the "cerebellum," and the huge size of the medulla oblongata (C 3, *m.ob.*). The seventh section (Plate III. fig. 11) is through the basioccipital, just missing the supraoccipital roof; it passes through the medulla oblongata (*m.ob.*), close behind the cerebellum: running askance, the razor has opened the ampulla of the left posterior canal, and has laid bare the canal through which the compound eighth nerve passes (*p.s.c.* 8). This section is from a less advanced specimen than that illustrated in figs. 2 & 3; the other structures severed in these sections will help to explain the movable machinery of the mouth and throat, which must now be described. In the profile and bird's-eye views of the primordial skull at this stage I have purposely excluded the delicate ectosteal laminæ, many

of which had commenced; but the relation of these can be best shown in the transverse sections, and my most important morphological business is the description and interpretation of the cartilaginous basketwork.

In Professor HUXLEY'S Croonian Lecture (Proc. Roy. Soc. Nov. 18, 1858, p. 29, fig. 8, *left hand woodcut*), the primordial skull of *Gasterosteus* is given at a stage corresponding to this; and in the 'Elements' another figure of this stage (p. 185, fig. 72, *A*) is given, with the remark that "this is the earliest condition of the cartilaginous cranium of the osseous fish that has yet been observed;" "but," the author goes on to say, "it can hardly be doubted that the hyo-mandibular and palato-quadrate cartilages have already deviated considerably from their primitive condition; and it would be a matter of great interest to ascertain whether these cartilages are primitively continuous, or whether, on the other hand, the hyo-mandibular altogether belongs to the second visceral arch, while the hinder crus of the palato-quadrate belongs to the first, but has become detached from its primitive connexion with the *basis cranii*." That passage was written in 1863; since then neither repeated discussions nor the light from other types that have been more or less fully worked out have given us any satisfactory solution of the question. I am gratified by knowing that the author is satisfied with the solution offered him; and I have here given *four* stages earlier than the one supplied by the young *Stickleback*. How admirably apt and simple are the metamorphic changes by which a few hooked and twisted rods of simple cartilage grow and change, splitting or coalescing, contracting or dilating, and thus by a few orderly morphological processes develop the most highly specialized face-apparatus to be seen in the whole circle of the Vertebrata! We have just seen how the circle of the eyes is finished, above, by the superorbital band, an *eave-like* band which connects the frontal *tent* with the ear-organ: we now come to the condition of the *sill* of the huge eye-space (Plate IV. fig. 1), a structure which has given the morphological student no little trouble. This second "præoral arch" does not continue distinct as in the Bird, but coalesces with the fore edge of its successor, the first "postoral." Articulating by a short "ligamentum teres," which leaves no joint-cavity, with the ectoethmoidal facet, this semilunar rod then thins out (figs. 1, 2, 3, see also Plate III. figs. 7, 8, 9, *pa.*), and running upwards applies its apical part to the "orbitar process" of the quadrate. In doing this it loses somewhat of its crescentic form, becoming *in-hooked* at its apex; thus it acquires, at last, the form proper to the species of arch to which it belongs*. The metapterygoid region (*mt.pg.*), not separated yet by ossification, has already acquired the form seen in the adult, being now flat and emarginate above. The rest of the pier of the first "postoral" is flat,

* If I have been able to get a lighted torch here it is not for the Fish only, as such, but *for use*, that the Bird, the Turtle, and many others may be understood. In the Bird the "orbitar process" is huge and gets outside and in front of the pterygoid, which, in articulating with the body of the quadrate, never fails to show an *apical process*; this epipterygoid hook is largest in the Grosbeak and in the Finches, its companions. In the "Testudinata" the pointed "orbitar process" merely touches the apex of the "epipterygoid columella;" whilst in Lacertians the process is aborted, and these arches are far apart.

until we come to the elegant quadrate condyle (*q.*), the angle of the "palato-quadrate arch." The hinder outline of the pier is so convex that the whole arch still retains the primordial curve, broken in upon by the oblique fissure which formed the joint-cavity. The "articulo-Meckelian rod" (mandible, *ar.*, *mk.*) is thick and produced into an angle behind the selliform hollow for the quadrate; it then continues thick and terete to its rounded end. The whole of the first postoral pier is let down so as to be below the expanded head of its successor (fig. 1), which now carries it. Thus simple is the morphological process by which the curious protrusible mouth of a fish is constructed!

The bony plates and the exact form, in section, of the mouth-margining cartilages are shown in the sectional views.

In the foremost of these (Plate III. fig. 7, *pa.*) the thick articular portion is shown to have at its infero-external face a delicate ectosteal lamina, the rudiment of the bony palatine. In the next (Plate III. fig. 8, *pa.*) the rod is flatter, and this is *behind* the bony plate. In the third (Plate III. fig. 9, *pa.*, *ms.pg.*) we have a perfect section of the mouth, and the palatine bar, much flattened, has a second bony lamina on its inner side, the "mesopterygoid."

The former, the palatine bony plate, has precisely the same relation in the young and old Sturgeon, and in old specimens the mesopterygoid is also well seen*. In the same section is seen the maxillary (*mx.*) and the Meckelian rod (*mk.*), perfectly round; on one side both the dentary and articulare (*ar.*) are seen, on the other only the dentary.

In the fourth section (Plate IV. fig. 7), which may be profitably compared to *two* similar views of the Tadpole's skull ("Frog's Skull," Plate VI. figs. 3 & 4), the coalesced "palato-quadrate" is cut through, the quadrate hinge being seen (*q.*) and the ascending pterygo-palatine bar (*p.pg.*). Below the quadrate is the articular region with its osselet (*ar.*), and beneath the section of the tongue and mouth-floor the crown of the inverted second "postoral" is cut through, showing the "basi- "hypo- and "cerato-hyals," in section and in relation. The great distance of the metapterygoid apex of the first "postoral" from the upturned postfrontal angle of the ear-sac is shown in the sixth section (Plate III. fig. 10, *mt.pg*); this part is *bent outwards*, the pier being in-bent where the two regions join: this is a correlate of the assumption of a new swinging-point, for the metapterygoid bends outwards to overlap the hyo-mandibular. Below the quadrate (*q.*) is the angular process of the articulare (*ar.*); below the back of the tongue (*t.*) is seen the fore end of the first basibranchial (*b.br.*), and on each side we see the "cerato-hyals" (*c.h.*) obliquely cut through.

Each hyoid ramus is now composed of four cartilages (Plate IV. fig. 1), which are ossified somewhat later than the arches in front; I did not find any traces of osseous deposit, even in transverse sections, highly magnified: the cartilages will now be described, and their osseous centres when I come to the seventh stage. To understand the state of things, reference must be made to the first splitting up of the "second postoral," and to the changes seen in the third and fourth stages; these have been just described.

* See my paper in Micr. Journ., June 1873, plate 20. fig. 5, *pa.*, *ms.pg.*.

But the hyo-mandibular (*h.m.*) showing yet no division by two osseous centres, and lying *behind* and not *within* the quadrate, is quite *Polypterine* in character. Reference to my second stage (Plate II. fig. 3, *h.m.*, *c.h.*), and to Dr. TRAQUAIR'S figures of *Polypterus* (fig. 6, *H.M.*, *H.M'.*), will give us an explanation of a peculiarity to be seen in that "Ganoid"—namely, that the top of the newly separated "cerato-hyal" (*c.h.*) of the embryo Salmon, which is connected with the lower end by a constricted portion, has its counterpart completely segmented off in *Polypterus*; and this it is which forms the accessory *hyo-mandibular* of TRAQUAIR (*op. cit.* p. 176); it is an "upper cerato-hyal." The term "post-hyomandibular" must not be used for this, but for the hinder condyle of the true "hyo-mandibular," a part which becomes so strangely modified in relation to the organ of hearing in the Frog ("Frog's Skull," Plate VII. fig. 13, pp. 170, 171). The head of the "hyo-mandibular" of the Salmon at this stage is slightly divided into two parts; but although many "Teleostei" have two condyles to this bone, in the Salmon the joint-cavity continues single. The "opercular knob" is at this stage a mere obtuse projection; the cartilage narrows gently towards it, and then suddenly; and here it curls forwards, getting a little within the metapterygoid flap; then, applying itself to the hind edge of the quadrate, it is really wedged between the quadrate and the angular process of the "articular" region. At the convexity of its bend, behind, we find a cupped space rather on the inside; it is for the stylo-hyal (*st.h.*), and a joint-cavity here makes this a small ball-and-socket joint. Below this joint the cartilage belongs to the "symplectic" region; it becomes the *nail* which is driven in a slanting manner into the inner face of the quadrate.

The "stylo-hyal"* (*st.h.*) does not appear until the emergence of the head from the egg (Fourth Stage, Plate III. figs. 1 & 6); it is evidently developed in the *hooked apex* of the posterior half of the primary hyoid bar in the fourth, and in the adult stage it is too short to show much of the curve, but *now* it is very evident. The apex of the anterior half develops the opercular process (see Plate II. figs. 3 & 6, Plate III. fig. 6, and Plate IV. fig. 1, *op.c.*). It is also to be noted that the *anterior half* of the bar forms the "hypohyal" below, which it loses, giving it up to the next half; whilst the posterior half keeps its own *apical* segment, the "stylo-hyal," and gains a new *distal* segment, the "hypohyal." These changes of *number*, *form*, and *place* are to me very wonderful; yet I must give my account of them in patient detail, not the less that my wit will not reach to their meaning. The elements of this half-arch are tied to each other by fibrous bands; I can find no joint-cavity between them. The stylo-hyal, true to its original character as an inturned hook, is articulated *inside* the apex of the great outflattened cerato-hyal; this piece (*c.h.*) only gets to be *two* by ossification, the upper third having the epihyal as a centre; but the "synchondrosis" is not severed through.

This piece is very flat above, with rounded margins; but it contracts and thickens below, and then forms a swollen head, which fits into a corresponding depression in the distal piece, the hypohyal (*h.h.*); this latter part is very solid and is grooved below

* These terms are purely *ichthyic*, and are not to be confounded with like terms used for the higher Vertebrata; we are not quite prepared yet for an harmonious terminology.

(Plate IV. fig. 7). Upon the two "hypohyals" the lingual element or basihyal (*g.h.*) rests in its hinder part; its fore part projects into the substance of the tongue.

The branchial arches (Plate IV. fig. 1, *br.* 1–5) are still unossified, but their basal elements are being fused together; the relation of the foremost piece to the floor of the mouth is shown in section (Plate III. fig. 10, *b.br.* 1), and the second pharyngo-branchial in its relation to the basis cranii is shown in another section (Plate V. fig. 5, *p.br.* 2): in this section part of the first cerato-branchial region is cut through (*c.br.* 1), and here also is shown the articulation of the "hyo-mandibular" beneath the ampulla of the "horizontal canal" (*h.m.*, *h.s.c.*).

Sixth Stage.—Young Salmon of the sixth week after hatching.

In Salmon of this stage there has been an increase in length less than might be supposed from a month's growth; they are three or four lines longer than in the fifth stage (about an inch and a sixth), but the yelk-sac has been entirely taken into the abdomen, and the tissues have become very much more perfect and solid. Ossification has begun in the parosteal tracts generally, and in most of the ectosteal, but we shall not find the bony plates of the sphenoidal region for some weeks to come; and most of the ectosteal plates will be best described in Salmon of the first summer. Yet there are changes of great importance that have already taken place in the cartilaginous skull, which is now beginning to pass from the *Polypterine* into the *Salmonine* morphological type. The vertical section (Plate V. fig. 2) is shown with the brain removed, and this must serve for comparison with both the inner and outer views of the fifth stage (Plate IV. figs. 1 & 4). The middle ethmoidal region is now much more developed and is very solid, the nasal sacs lying, as in the Sturgeon, in little recesses or crypts on either side. The trabecular cornua are only separate at their ends by a very small emargination; these, and the septum common to both the nasal and anterior orbital region, are formed of continuous cartilage. This section, which is a little more than half, being made to the left of the exact mid line, shows what is most instructive, namely a *double origin* for the interorbital cartilage. The "mesoethmoid," besides being continuous with the prosencephalic cartilaginous roof, also sends a sharp, wedge-like lamina *backwards* into the presphenoidal region; and besides this the coalesced tilted trabeculæ have sent *upwards* another lamina, which runs from the ethmoidal to the basisphenoidal region, some distance below the presphenoid. Here, evidently, we are beginning to get a clue to the remarkable characters of the Bird's skull, in which the differentiation of morphological regions often takes place some days after the formation of continuous hyaline cartilage over several truly distinct parts. In the Bird (*chick*) the distinctness of the trabeculæ from the "investing mass" is best shown during the second week of incubation, and the morphology of the interorbital plate is best studied at the beginning of the third. I have shown this breaking up of large parts of the cartilage into more or less distinct morphological elements in the "shoulder-girdle" in my memoir on that part of the Vertebrate skeleton; and it must not be supposed incredible that morphological differentiation of the skull may

often not be exhibited until the cartilage has in many cases been converted into bone. The skull of a Shark and that of a young Rodent (after the osseous centres are all formed) may be profitably compared together; for it would seem that in the Mammalia alone does the skull perfect its segments—segments altogether so unlike those which form the rest of the axis, and which are most truly primordial*.

The membranous interorbital space in the young Salmon is the equivalent of the "fenestra" in the Bird, formed by retreat of the ethmo-presphenoidal cartilage from the trabecular crest. In *Pelecanus onocrotalus* both the præoral arches behave in a similar manner; both coalesce in front of the elbowed part, and both of these double bars send upwards an azygous keel. I shall have to return to this comparison in describing the next stage. The trabecular carina only reaches to the converged part of the trabecula; the ethmo-presphenoidal wedge only takes up the front third of the prosencephalic (anterior sphenoidal) region (Plate V. fig. 2). The cranial roof is thicker, and extends further over the middle cerebral lobe than in the last stage, and the band which unites the roof to the ear-capsule is broader and shorter. The alisphenoidal region is beginning to be walled-in by a growth of cartilage *downwards* from the *band*, and forwards and inwards from the ear-sac; for the rest, this region is membranous, as in the Lacertilia. The Lizards have an orbito-sphenoid *mapped out* by an outline of partly ossified cartilage, and the band at the top of this region answers, as far as it goes, to the *very edge* of the roof-cartilage of the young Salmon; but there is no band running to the periotic region, and the only probable rudiment of an alisphenoid in the skulls in my collection is a small *epiphysis* at the antero-superior angle of the prootic in a Mexican Lizard (*Læmanctus longipes*). In the young Salmon the anterior sphenoidal region, although well roofed-in, has no cartilage in its side walls, as in the *carinate* Birds and "Struthionidæ," with the exception of *Struthio*. The "fontanelle" is still very large (*fo.*), yet the superoccipital cartilage (*s.o.*) reaches to the junction of the anterior and posterior semicircular canals (*a.s.c.*, *p.s.c.*). How large these and the other parts of the labyrinth are the figure shows, and also how the periotic cartilage fails to enclose the ampullæ and most of the arch of the anterior and posterior canals, as well as the "utriculus" (*ut.*) and "sacculus" (*sc.*). The strong sheath of the notochord is now beginning to be ossified, and thus to lay the foundation of the "basioccipital," *but of it alone*; the posterior part of the investing mass" (*iv.*) forms additional substance for the completion of this *quasi centrum*. The roof-bones are not shown in this figure, except the "superethmoidal lamina;" the premaxillary is also cut through; and the long "parasphenoid" has now the "vomer" beneath its fore end, and to it are attached a number of teeth.

A section (Plate V. fig. 3) immediately in front of the projecting "ectoethmoidal wings" (prefrontal lobes) shows at this stage a very complete coalescence of the upgrowths

* In all generalizations of this sort the *Amphioxus* is left out of the question; when we obtain links that will in any way bind it to the Myxinoids, then we may begin to reason from a higher stand-point (see "Frog's Skull," p. 202).

of the trabecular horns, and the width and thickness of the subnasal lamina just in front of the facet for the palatine; the skull now at this part is very *Acipenserine.* In this section the nasal sacs are severed at their opening, the lateral parts of the premaxillaries are cut through, the fore part of the parasphenoid, and the "prepalatine" bar with its ectosteal plate. Another section (Plate V. fig. 4), made near the fore part of the orbits and a little obliquely, shows on one side part of the antorbital (ectoethmoidal) plate, and on the other the *roof-cartilage.* This is a most instructive section, and should be compared with a similar section of the Fowl's skull made at the beginning of the third week of incubation ("Fowl's Skull," Plate LXXXIII. fig. 11, *p.s.*, *i.o.s.*, *b.s.*): for the crest growing down from the roof is the "mesoethmoid" passing into the presphenoid; the roof itself ends in the Bird in a spike above the olfactory groove, and in the young Salmon in the free, retral, median lobe. Below, the tilted coalesced trabeculæ send up their crest, in which the lower part of the "mesoethmoid" passes *below* the presphenoid into the basi-sphenoidal region; this will be better understood in the next stage. Here we see the raised middle of the "parasphenoid" applying itself to the trabecular groove and the tilted and broad "mesopterygoid" region of the subocular arch (*pa.s.*, *pa.*). In another section (Plate V. fig. 1), made through the fore part of the auditory capsule, we see the ampulla and part of the arch of the anterior canal (*a.s.c.*) overlying the hyo-mandibular (the fore part of which is cut through), and forming the tegmen tympani. Here the skull is widest, for it covers in the posterior part of the middle lobe of the brain, where it overlaps the posterior region; here was seen, inside the ampulla of the anterior canal, the Gasserian ganglion (5). The posterior branch of this fifth nerve is seen passing through its own foramen in the "prootic" cartilage; and the fore part of the investing mass, confluent with the ear-cartilage, is undergirded by the "basitemporal wings" of the parasphenoid, over which lie the orbital muscles (*o.m.*). Here also is well seen the manner in which the periotic cartilage is folded over the semicircular canal, but fails to wall it in; the sharp edge above is that which runs into the boundary-band that comes from the sides of the cartilaginous roof.

Seventh Stage.—Young Salmon of the first summer, $1\frac{1}{2}$ *to* $2\frac{1}{4}$ *inches in length.*

We have now come to a stage in which the Ganoid characters are being rapidly effaced, whilst that which is "Teleostean" has become apparent. In this arbitrary but not non-natural *seventh age* of the Salmon we are able to detect not only the *intermediate* laminæ of bone in which the cartilaginous skull is arrayed, and by which, as in proven armour, its possessor takes a high ichthyic rank, but we have now rudiments, at least, of all the *deep* laminæ that graft themselves upon the cartilage within. The cartilaginous skull itself has become much more massive, and it is no hard task now to harmonize the skull of the young with that of the adult. Holding in mind the condition of the last stage (Plate V. figs. 1, 2, 3, 4), we see that the cartilaginous roof is increasing in thickness, and extending backward over the middle cerebral region, whilst the sharp edges of cartilage (behind from the occipital ring, and postero-laterally from the cartilaginous ear-sacs)

are growing more over the third vesicle and cerebellum. The roof-cartilage is thicker (fig. 10) and has developed an inturned selvedge, which encroaches upon the membranous orbito-sphenoidal region, whilst the "mesoethmoidal" wedge has grown further backwards along the presphenoidal line. A thin spicule of bone has been formed over the "ectoethmoidal wing" (figs. 7 & 9, *l.e.*), and this does not behave like the "supra-ethmoidal" plate (fig. 6, *n.**), but grafts itself upon the cartilage and becomes the so-called "prefrontal" bone. In the prosencephalic region I have not figured the permanently distinct frontals above; but laterally there are now a pair of new bones to be illustrated (figs. 6, 7, 9, 10, *o.s.*). These laminæ are like the valves of bivalved "Entomostraca," and occupy already nearly the whole of the orbito-sphenoidal space. These bones curiously illustrate, and are illustrated by, their counterparts in two very diverse types of Vertebrata: they have precisely the same character, as bones, as those developed over the "orbito-sphenoidal" cartilage of the Sturgeon; there, however, they continue as distinct "investing bones," even to old age (see adult Sturgeon's skull, with soft parts modelled, in Mus. Coll. Surg.). In the Fowl, at the time of hatching, the orbito-sphenoidal region ("Fowl's Skull," Plate LXXXIV. figs. 7 & 8, *p.s.*) is entirely membranous; it has no alæ growing from the presphenoid (ibid. Plate LXXXIII. fig. 11, *o.s.*, *p.s.*); but in a few weeks *two* membrane-bones appear on each side, and these soon graft themselves upon the presphenoid (see also Plate LXXXVI. figs. 11 & 14, and Plate LXXXVII. figs. 1 & 2, *o.s.*, *p.s.*). The *single* bone in the young Salmon grafts itself also upon the presphenoid exactly in the same way (Plate V. figs. 6, 7, 9, 10, *o.s.*, *p.s.*); and not only so, but the upper edge of each plate splits and embraces the descending roof-plate (fig. 10). That this is not done in the case of the Bird also, depends upon the fact that the "culmen cranii" growing backwards from the "ethmoid" is arrested midway (ibid. Plate LXXXIII. figs. 2, 4, 5, Plate LXXXIV. fig. 7, Plate LXXXV. fig. 1, and Plate LXXXVI. figs. 11 & 14, *o.s.*, *eth.*). There is no difficulty now in understanding the meaning of the great interorbital bone of the adult Salmon (Plate VII. figs. 3, 4, 10, *o.s.*), nor in seeing why it is arrested in its growth downwards; in like manner the *distinct* presphenoid of the Fowl (*op. cit.* Plate LXXXVII. fig. 1, *p.s.*) reaches no further downwards than to the top of the *trabecular keel*, in which the mesoethmoidal and basisphenoidal ossifications meet. Now we know that the *primordial* "notch" between the upper and lower retral median cartilages that grow from the ethmoid in the Salmon answers to the *secondary* "fenestra" of the Bird, it becomes a question of intense interest as to what the lower bar is, as well as how it comports itself. *Here*, in the Salmon, there is no median ethmoidal ossification; *there*, in the Bird, the basisphenoid borrows its ossifying centre at first from the parasphenoid, a bone permanently distinct in the Fish, but the median ethmoid becomes an immense bone (*op. cit.* Plate LXXXVII. fig. 1, *eth.*), all arising from a single centre†.

But the *prepituitary* part of the basisphenoid is formed, as to cartilage, in the same

* The "mesonasal" is lettered *n* by mistake in these figures (2 and 6); it is marked *eth.* in the rest.

† Not in the "Ratitæ," however (see "Ostrich's Skull," Plates VIII.–XIV.); here the *roof* is separately ossified.

way—namely, by the extension backwards *below the optic nerves* of the "trabecular crest." In the Bird this crest ("Fowl's Skull," Plate LXXXIII. fig. 14, *b.s.*) expands in front of the pituitary body into the "anterior clinoid wall" (Plate LXXXIII. fig. 2, *a.cl.*). In the Fish the trabecular crest runs into the pituitary space, *between* the out-bowed part of the trabeculæ (Plate V. figs. 6 & 7). Thus the foundation of the clinoid wall is laid in cartilage, but the wall itself is finished in another way. The membranous septum *behind* the optic nerves becomes partially ossified; this osselet is a Y-shaped little *prop*, the arms of which seize the lower edge of the alisphenoids, and the leg of which is implanted upon the rounded end of the trabecular crest (Plate V. figs. 6 & 7, Plate VII. figs. 3 & 4, and Plate VIII. figs. 2, 3, 4, *b.s.*). At first (Plate V. figs. 6 & 7) the foot of the bone does not reach the cartilage, but they grow towards each other afterwards. This bone is a *prepituitary* "basisphenoid;" it is a deep lamina or "ectostosis," and it becomes one with the primordial skull both above and below. Immediately behind this bone the pituitary body (Plate V. figs. 6 & 7, *py.*) descends to reach the "parasphenoid;" there is no other *seat* to the "sella turcica;" and on each side the internal carotid artery (*i.c.*) enters.

Before leaving the fore part of the skull I may refer to the extraordinary expansion which the trabeculæ have already undergone. At first (Plate I. figs. 1 & 2, *tr.*) they were filiform thickenings; they soon (fig. 5, *tr.*) spread into a bifoliate form; the "bifoil" has already become differentiated into a "meso-" and an "ectoethmoidal" region. Now see what has taken place! Between the eyes we have the grooved interorbital base (Plate V. fig. 9), then the wide floor of the "ectoethmoid" with the "palatine *facets*," then the floor of the nasal sacs, and, lastly, the emarginate trabecular plate formed by the trabecular horns (ethmo-vomerine cartilage of HUXLEY). Above, the lateral parts have grown into the sloping prefrontal wings, which meet in the *roof-cartilage*, whilst along the mid line there grow backwards those two most important crests, the "ethmo-presphenoidal" and the "trabecular."

We never see a *cranium* pure and simple; for the outgoings and incomings of nervous force there are required appropriate organs that either nestle under the eaves of the skull or are projected into its walls. All the space from the great fifth nerve to the *compound* eighth is occupied by the antechambers, chambers, and galleries of the ear-organ; here no fence but membrane and a gelatinous stroma is interposed between the brain and the labyrinth. But the skull on the outside becomes exceedingly strong by this impaction of the organs of hearing; the rudiments of the thick bony blocks that exist in this part of the adult are now to be seen as their "ectostoses." But the auditory region is fringed on its anterior margin by a slight cartilaginous growth, the thick upper selvedge of which is formed by the "superorbital band;" this fringe is undergoing ossification, and is the "alisphenoid;" as I have just mentioned, it is underpropped by the Y-shaped bone. This is a very unfinished skull as far as the sphenoids are concerned, and has little in common with what we are all familiar with in the human skull and in that of the Mammalia generally. In the Mammalian skull all that part of the

anterior sphenoid occupied by the "culmen cranii" is membranous, and the membranous orbito-sphenoids of the Salmon are represented by cartilage in the Mammal. Again, the alisphenoids of the young Salmon are scarcely more free from the ear-cartilage than the laminar growth of the prootic region in an average Mammal (see in the Beaver, HUXLEY'S 'Elem.' p. 245, fig. 97, *as.*, *pro.*); but where the alisphenoid of the Mammal thins out above, there in the Fish it has a thick selvedge, connecting it both with the ethmoidal roof and the periotic capsule. The basisphenoidal region is also in a most rudimentary and, as it were, fragmentary condition; for there is a feeble prepituitary portion, an open *sellar* space, and the cartilage (*basilar*) which should form the posterior clinoid wall, the postpituitary region, and the spheno-occipital synchondrosis,—all this is trespassed upon by the "prootic bones," which borrow it to form their curious basi-cranial bridge.

Relatively to the rest of the skull the auditory capsules are very large; their centres of ossification are curiously placed—one on the anterior margin behind and above the main part of the fifth nerve, and perforated by the posterior branch, and the other *four* forming a *right*-angular series along the most projecting part, covering the galleries of the labyrinth (Plate V. fig. 7). The first is the "prootic" (*pro.*); the second, which is over the ampulla of the anterior canal, is the "sphenotic" (*sp.o.*); the third, over the ampulla and arch of the horizontal canal, is the "pterotic" (*pt.o.*); the fourth, over the arch of the posterior canal, is the "epiotic" (*ep.*); and the fifth, which is over its ampulla, is the "opisthotic" (*op.*). Of these Professor HUXLEY is responsible, as to nomenclature, for *three*, the "tria ossicula" of KERKRINGIUS, who described them in the human skull (see HUXLEY'S 'Elem.' p. 153); the other *two* which I contend for are the "sphenotic" and "pterotic." At present these bones are in their infancy, the cartilage is whole beneath them; it still retains the impressure and form of the elegant and large elements of the labyrinth. The most exquisite part of this cartilaginous capsule is seen beneath the "tegmen tympani" and facet for the "hyo-mandibular;" this is the ovoidal pouch for the "sacculus," which lies between the foramen for the "portio dura" (7^a) and that for the compound eighth nerve (8). The antero-superior part of this "saccular recess" is occupied by an *oval fenestra*, the primordial deficiency already described (see Plate II. fig. 4); it does not, however, persist, but closes as in the third stage of the Frog, and does not reopen as in that air-breathing type (see "Frog's Skull," Plate IV. fig. 7, and Plate V. figs. 1 & 4, *au.*, *st.*). That out-bent part of the trabeculæ, the *apical* part which joins the "investing mass," is still present, but is a temporary structure; thus the three anterior facial arches all escape away from their primary relations to the base and sides of the cranium. The lowered position of the pterygo-palatine and mandibular arches is shown in the next figure (fig. 8; *the rest of the face detached from the skull*, fig. 7).

The "superoccipital" region is now invested by an ectosteal lamina, and the "foramen magnum" is bounded laterally by a pair of crescentic ossicles, the exoccipitals (Plate V. figs. 6 & 7, *so.*, *eo.*).

The ossified sheath of the notochord (*nc.*, *bo.*), the median, hollow, styloid rudiment of the "basioccipital," has not much affected the posterior half of the "basilar plate," as yet*.

One of the peculiar characters of the palato-pterygoid bar is its projection beyond the prefrontal attachment; it is a part well marked in the newly metamorphosed Frog ("Frog's Skull," Plate VII. fig. 11, *pr.pa.*). The Lamprey, evidently related to the prototype of the Frog, has it also in the same degree (MÜLLER, 'Myxinoids,' pl. 4. fig. 3, *under view*), although in that low Fish the half-suppressed bar corresponds on the whole with my fifth stage, or Tadpoles that have begun to acquire limbs.

The long suppression and the secondary character of this bar made me waver for a long while as to the true morphological character of this arcade; but I have no doubts left now, and shall speak of it unhesitatingly as the "second præoral arch." The prepalatine spur is normal enough when it is regarded as the terminal part of a facial rod; and the points of attachment of this bar are easily understood to be consistent with the *habit* of these arches generally, as they are always catching hold of each other to form a basketwork. Posteriorly this bar does not connect itself with the trabeculæ, as in the Lizard and the Bird, but its apex is completely fused with the fore edge of the pier of the mandible, with the well-known "orbitar process." *Under* the fore part the palatine ectostosis (Plate V. fig. 8, *pa.*) bearing teeth has begun to invest the cartilage; *below* the hinder part, and more within than without, is the "pterygoid" plate (*pg.*); and *over* the middle part is the "mesopterygoid," an ovoidal shell of thin bone with its hollow face looking inwards (*m.pg.*)†.

At the apex of the lowered mandibular pier the ear-shaped "metapterygoid" (*mt.pg.*) has worked into the fore half of the cartilage; and below the "quadratum" (*q.*), which began on the *outside*, as in the Frog, Newt, and Lepidosiren, has grown to a very elegant flabelliform bone with a *periosteal* posterior wing that is grooved on its inner face, and into which the symplectic is inserted obliquely, like a badly driven nail. The unossified quadrate angle forms an elegant condyle, which fits into a deep fossa in the "articular" end of MECKEL'S cartilage; this, with its largely projected angle, is very much like the human "ulna;" the joint is a simple hinge. In front of the angular and articular region MECKEL'S cartilage retains its old cylindrical form, and has its rounded end incurved as at first. Much of the lower edge is occupied with a lanceolate "articulare" full of spongy hollows, the primary lamina subdividing again and again (see Fifth Stage, Plate III. fig. 9, *ar.*).

The "hyo-mandibular" (*h.m.*), although made now the common suspensorium of these

* It is easy to see that if the vertebrate animal had been, in each or any case, *anencephalous*, then the materials were at hand, in the notochord, its sheath, and the basilar plate, for several vertebræ, which would have elegantly diminished in size from behind forwards; the tantalizing *Amphioxus* merely throws a "will-o'-the-wisp" light on this dark margin of vertebrate morphology.

† In determining these bones in other types, it should be recollected that the "palatine" plate is *under* and *outside*, the "mesopterygoid" *over*, and the pterygoid *under* and *within*; this may help the palæontologist with his "Ganoids" and other extinct types.

massive bars, is as yet not over large, as we see it in the adult; its long process has now the proper "symplectic" bony sheath (*sy.*), in addition to the other ectostosis on the main part. The opercular knob (*op.c.*) is large and well defined. The synchondrosis below the two bones is hollowed inside and behind for the head of the short "stylo-hyal" ray (*st.h.*), which is now enclosed in its own bony sheath. The lower end of the "stylo-hyal" is attached by a fibrous cord to the next cartilaginous bar, which has two ectosteal sheaths (the "epihyal" and "cerato-hyal" proper, *ep.h.*, *c.h.*). The rounded cerato-hyal end fits into the cupped surface of the thick bulbous distal "hypohyal" (*h.h.*); there is no joint cavity between them. There is a cavity, however, between the hypohyal and the azygous piece, the keystone of the arch; this is the *glossal bone*, or true "basihyal" (*g.h.*); it has now a dentigerous bony lamina, its proper ectosteal plate, whilst the hypohyal, short as it is, has two centres of ossification.

As this present paper is merely the first of a series which I hope to offer to the Royal Society on the Fish's Skull, I shall refrain from making any SUMMARY. The Teleostean must be studied in the light of the other ichthyic types; there is the more need for this, as it is, indeed, the most specialized of all. When the "Marsypobranchs," "Elasmobranchs," "Dipnoi," and "Ganoids" are thoroughly worked out it will be easy to summarize the facts obtained. With regard to the Salmon itself, the reader is referred to a very important work on its structure by Dr. CARL BRUCH, 'Vergleichende Osteologie des Rheinlachses (*Salmo salar*, L.) mit besonderer Berücksichtigung der Myologie, nebst einleitenden Bemerkungen über die skelettbildenden Gewebe der Wirbelthiere' (Mainz, 1861).

DESCRIPTION OF THE PLATES.

PLATE I.

First Stage.—Embryos from the egg with simple facial arches.

Fig. 1. Lower view of head, with facial arches shining through. ×20 diameters.
Fig. 2. Upper view of same specimen, with skin partly removed. ×20 diameters.
Fig. 3. Lower view of another head, partly dissected. ×20 diameters.
Fig. 4. Upper view of head, undissected. ×20 diameters.
Fig. 5. Another upper view, dissected. ×20 diameters.
Fig. 6. Side view of head within chorion. ×20 diameters.
Fig. 7. Another head, seen from below (dissected). ×20 diameters.
Fig. 8. Part of section of egg with contained embryo, cut longitudinally. ×20 diameters.
Fig. 9. Head of another embryo, obliquely shown. ×20 diameters.
Fig. 10. Transverse section, through the eyes, of an unusually symmetrical embryo. ×26 diameters.
Fig. 11. Another transverse section, further back. ×26 diameters.

PLATE II.

First Stage (continued).

Fig. 1. Section, through the eyes, of an unsymmetrical embryo. $\times 24$ diameters.
Fig. 2. Another similar section, further back. $\times 24$ diameters.

Second Stage.—Embryos with hyoid arch split up.

Fig. 3. Under view of head, somewhat depressed. $\times 24$ diameters.
Fig. 4. Under view of same head, with postoral arches removed. $\times 24$ diameters.
Fig. 5. Part of another skull. $\times 30$ diameters.

Third Stage.—Mandibular arch segmented.

Fig. 6. Lower view of skull and face, with branchial arches removed. $\times 24$ diameters.
Fig. 7. Same object, upper view. $\times 24$ diameters.
Fig. 8. Branchial arches of same, separately shown, from below. $\times 24$ diameters.

Fourth Stage.—Head emerging from the chorion, and hatched embryos.

Fig. 9. Front view of head. $\times 20$ diameters.
Fig. 10. Section of the same, through the eyes. $\times 20$ diameters.
Fig. 11. Upper view of head. $\times 10$ diameters.

PLATE III.

Fourth Stage (continued).

Fig. 1. Side view of head, with face dissected. $\times 25$ diameters.
Fig. 2. Lower view of same, dissected. $\times 25$ diameters.
Fig. 3. Section of head of partly hatched embryo. $\times 20$ diameters.
Fig. 4. Side view of head of hatched embryo. $\times 20$ diameters.
Fig. 5. Section of the same. $\times 20$ diameters.
Fig. 6. Primordial skull of same, from above. $\times 25$ diameters.
Fig. 7. Section of ripe embryo-head through nasal sacs. $\times 25$ diameters.
Fig. 8. Another section through prosencephalon. $\times 25$ diameters.
Fig. 9. Another through the same, and also the eyeballs. $\times 25$ diameters.
Fig. 10. Another section, behind the eyes. $\times 25$ diameters.
Fig. 11. Another section, behind the left ear-sac. $\times 25$ diameters.

PLATE IV.

Fifth Stage.—" Fry" the second week after hatching.

Fig. 1. Side view of primordial skull. $\times 24$ diameters.
Fig. 2. Upper view of same. $\times 24$ diameters.
Fig. 3. Lower view of same. $\times 24$ diameters.
Fig. 4. Vertical section of the head. $\times 24$ diameters.
Fig. 5. Part of same section. $\times 48$ diameters.
Fig. 6. Another vertical section (part) a little to the right. $\times 24$ diameters.
Fig. 7. Section through the eyes (*of fourth stage*). $\times 25$ diameters.

PLATE V.

Sixth Stage.—Young Salmon of the sixth week after hatching.

Fig. 1. Transverse section through anterior part of auditory capsule. $\times 20$ diameters.
Fig. 2. Section of head (vertical). $\times 16\frac{1}{2}$ diameters.
Fig. 3. Transverse section through nasal sacs. $\times 20$ diameters.
Fig. 4. A similar section through fore part of orbit. $\times 20$ diameters.
Fig. 5. Section through ear-sac (*fifth stage*). $\times 20$ diameters.

Seventh Stage.—Young Salmon of the first summer, $1\frac{1}{2}$ *to* $2\frac{1}{4}$ *inches long.*

Fig. 6. Vertical section of head. $\times 15$ diameters.
Fig. 7. Side view of skull. $\times 15$ diameters.
Fig. 8. Facial bars of same. $\times 15$ diameters.
Fig. 9. Lower view of face. $\times 20$ diameters.
Fig. 10. Section of fore part of skull. $\times 15$ diameters.

PLATE VI.

Eighth Stage.—Adult Salmon.

Fig. 1. Side view of skull and face. Nat. size.
Fig. 2. Same, with outer bones removed. Nat. size.
Fig. 3. First branchial arch. Nat. size.
Fig. 4. Second branchial arch (part). Nat. size.
Fig. 5. Lateral view of basibranchiostegal. Nat. size.

PLATE VII.

Eighth Stage (continued).

Fig. 1. Upper view of skull with bony plates on. Nat. size.
Fig. 2. The same, from below. Nat. size.

Fig. 3. Side view of skull, with bony plates removed. Nat. size.

Fig. 4. Vertical section of skull and bony plates. Nat. size.

Figs. 5–11. A series of transverse sections of skull, with bony plates on. Nat. size.

PLATE VIII.

Eighth Stage (continued).

Fig. 1. Skull, from above, bony plates removed. Nat. size.

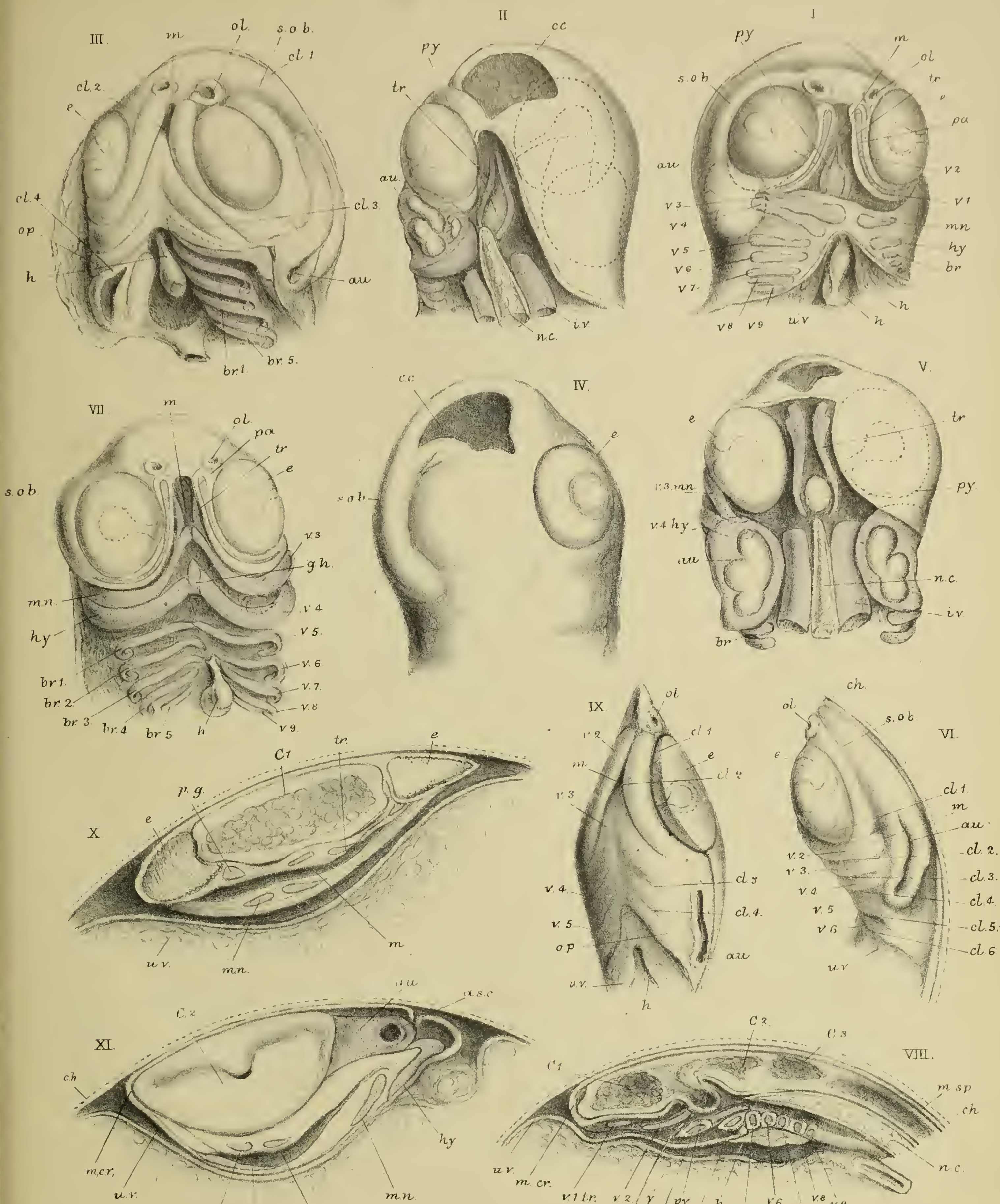
Fig. 2. The same, from below. Nat. size.

Fig. 3. Part of a vertical slice of the skull. Nat. size.

Figs. 4–7. The rest of the series of transverse sections. Nat. size.

Fig. 8. End view of skull. Nat. size.

Fig. 9. Inner view of facial arches. Nat. size.



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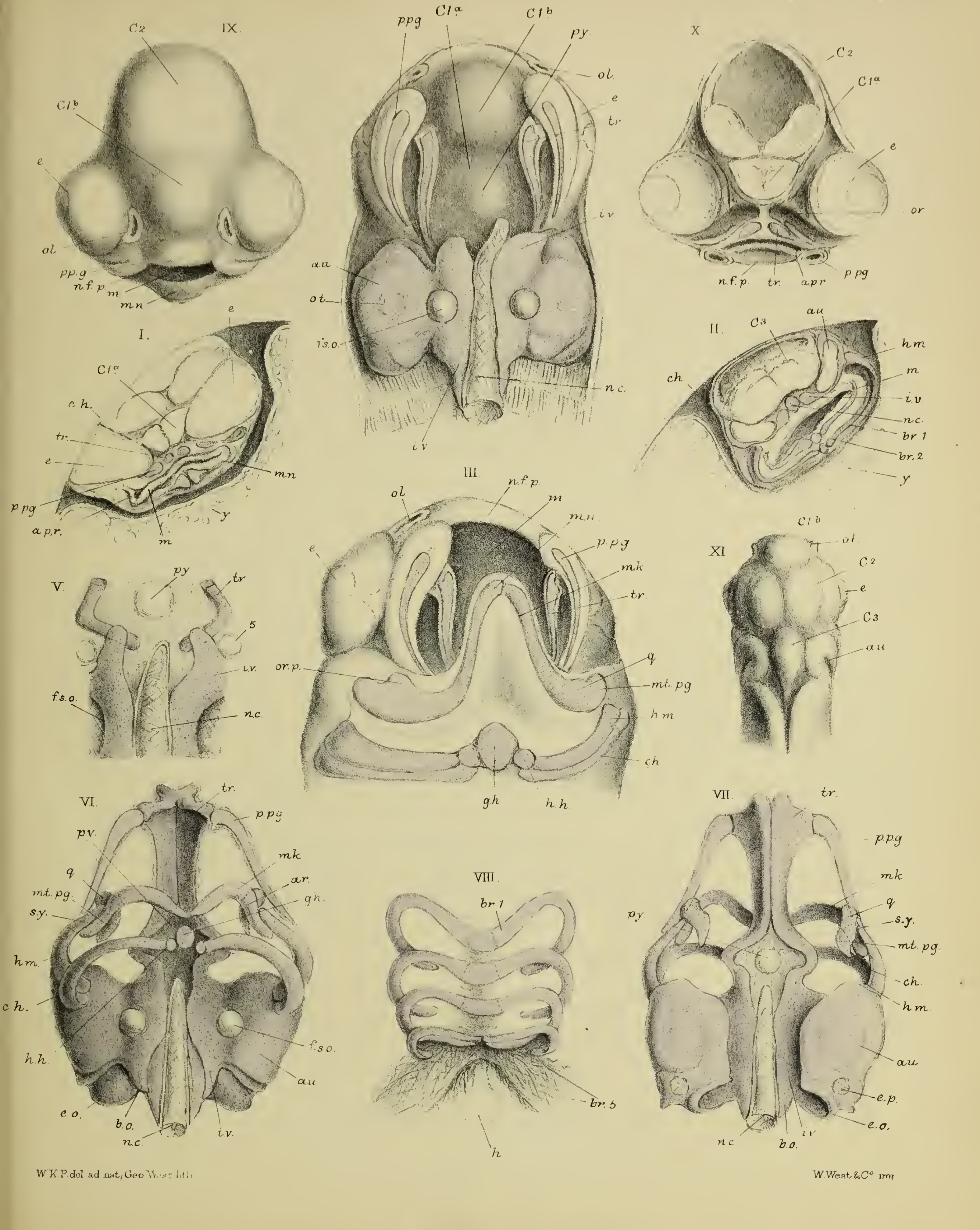
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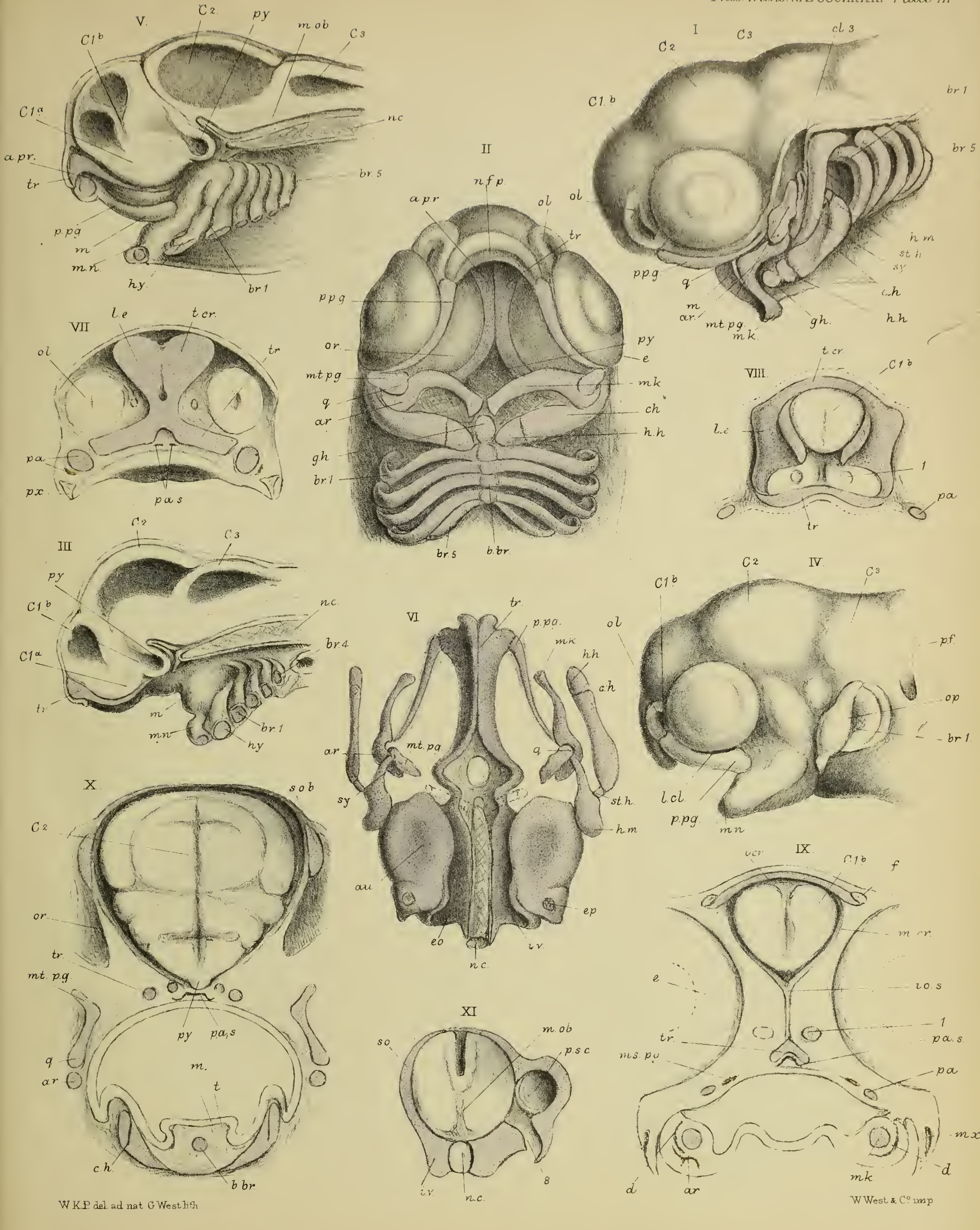
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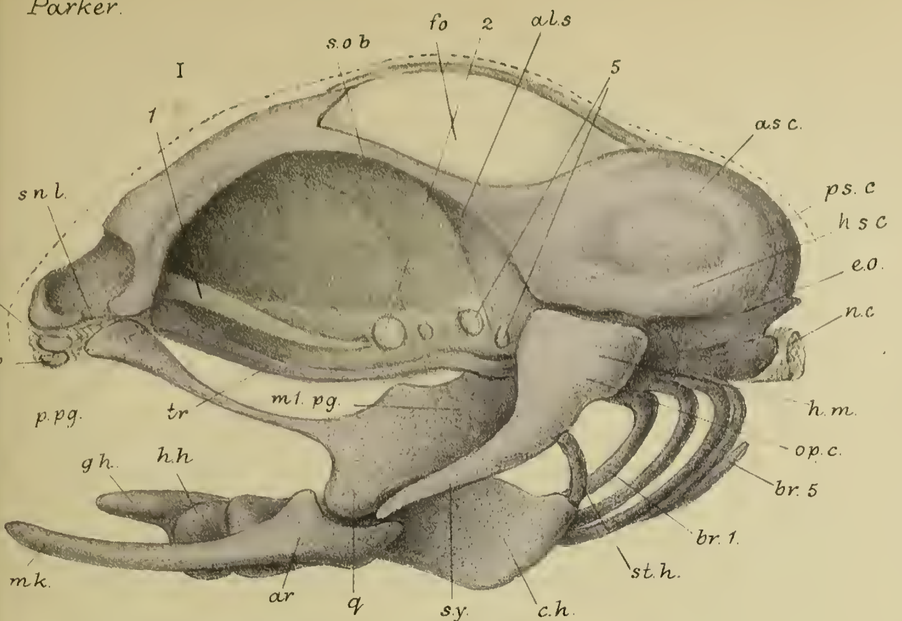

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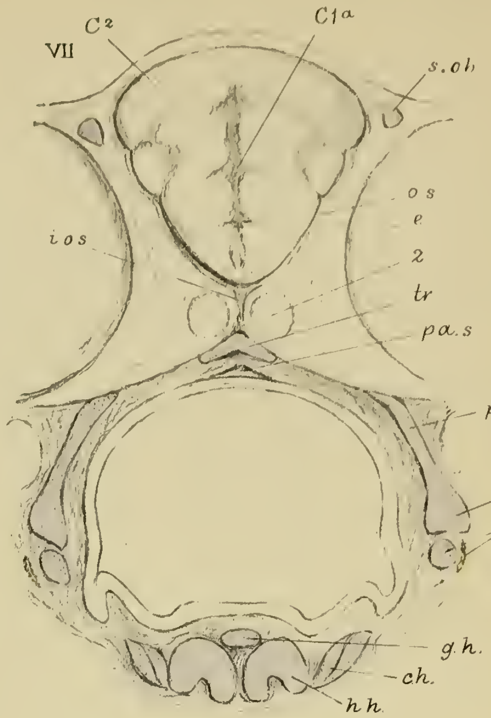

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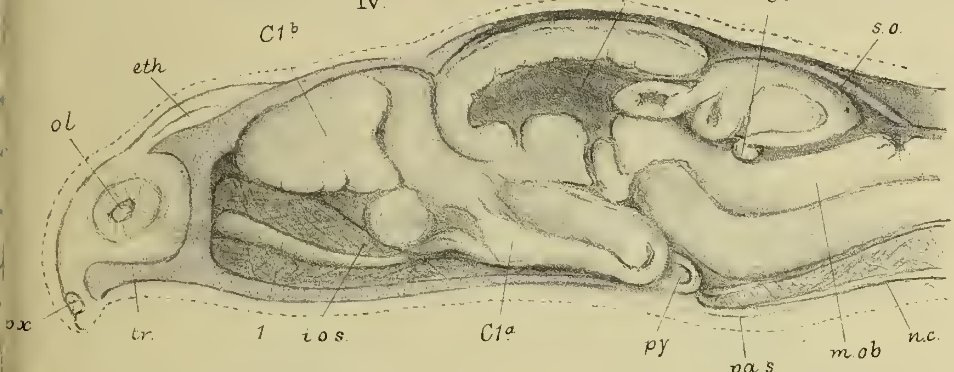

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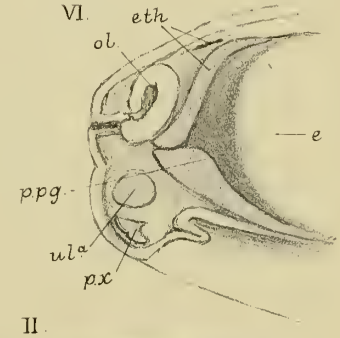

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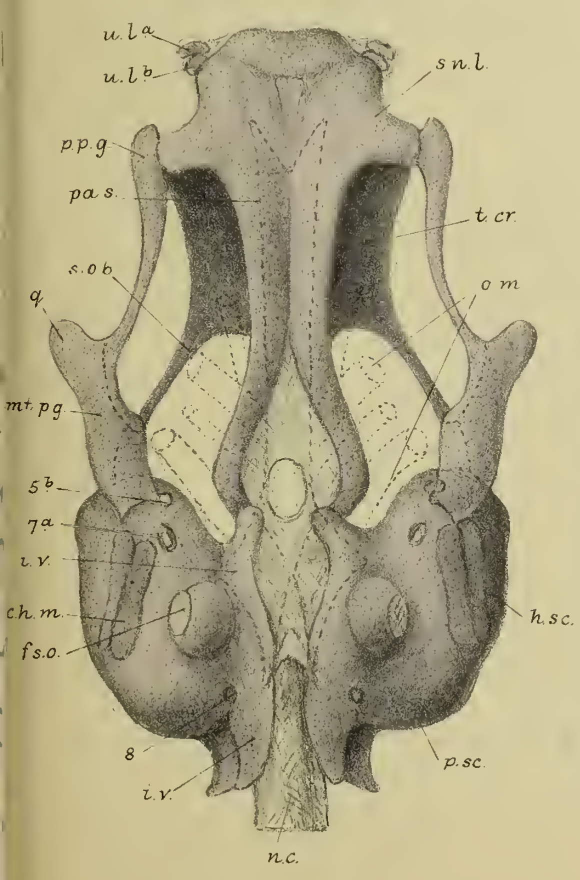

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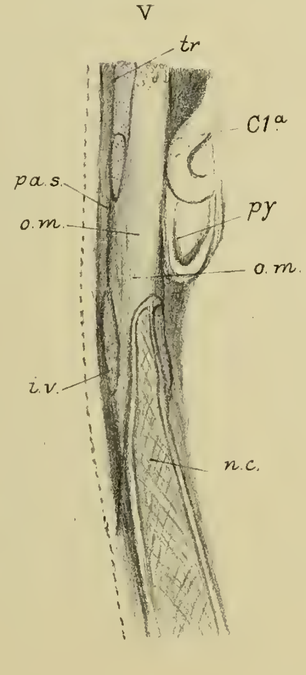

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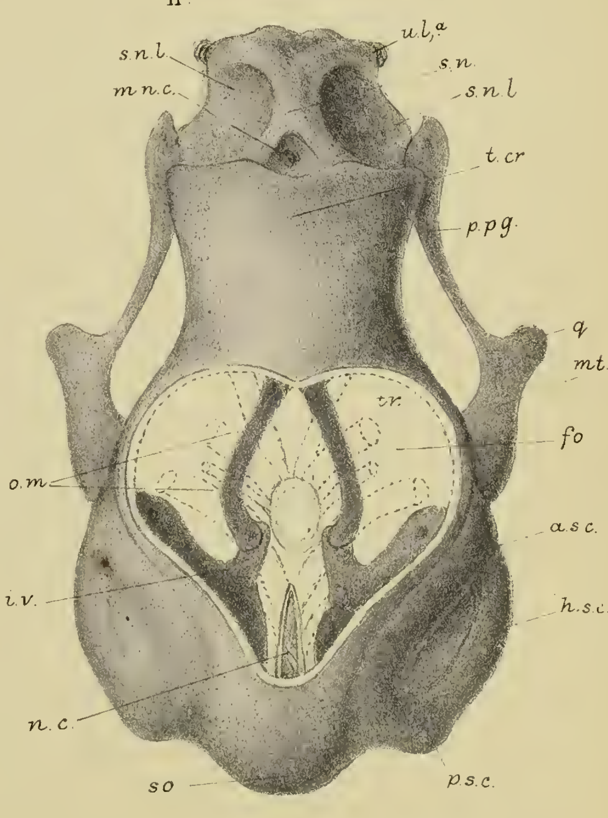

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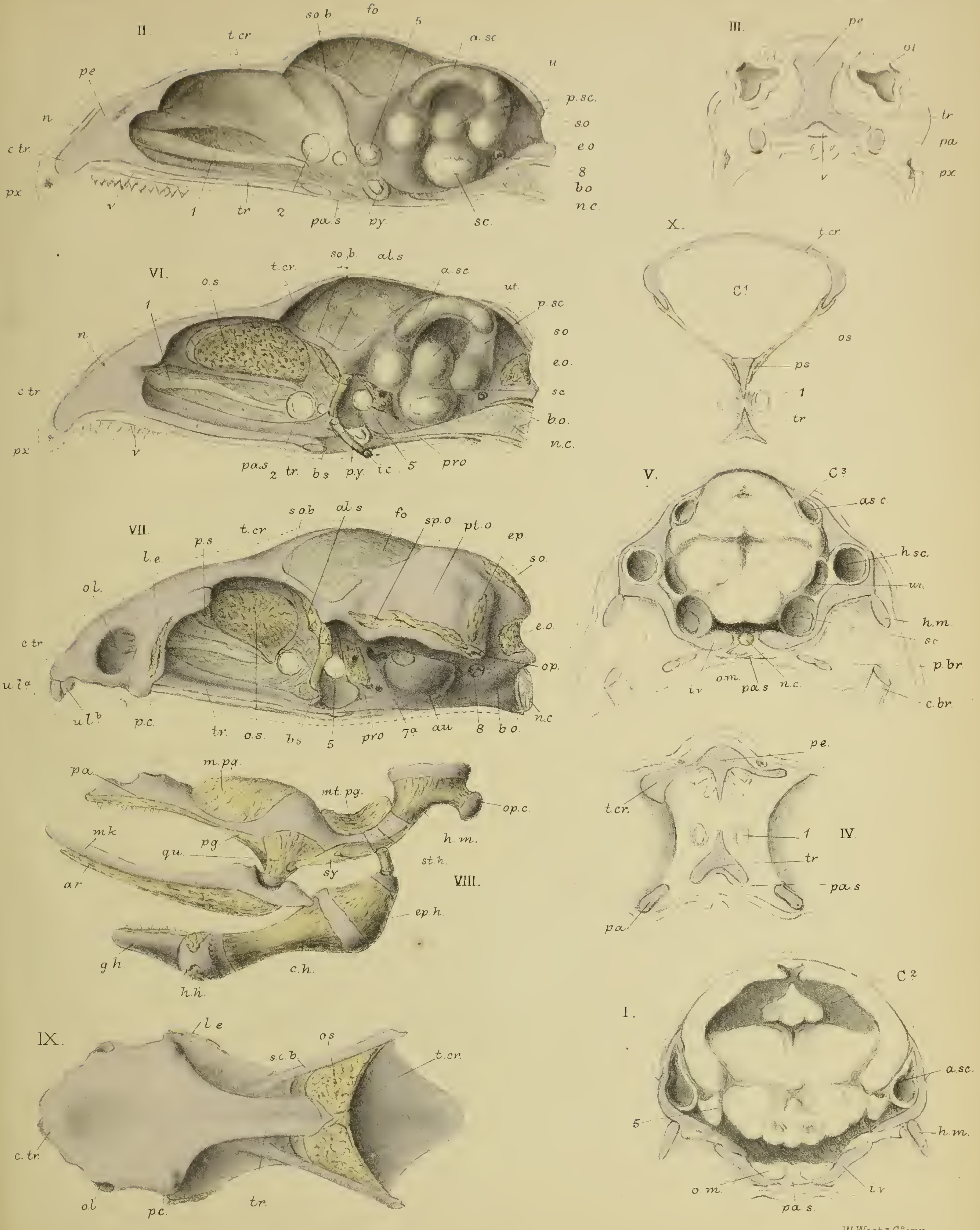

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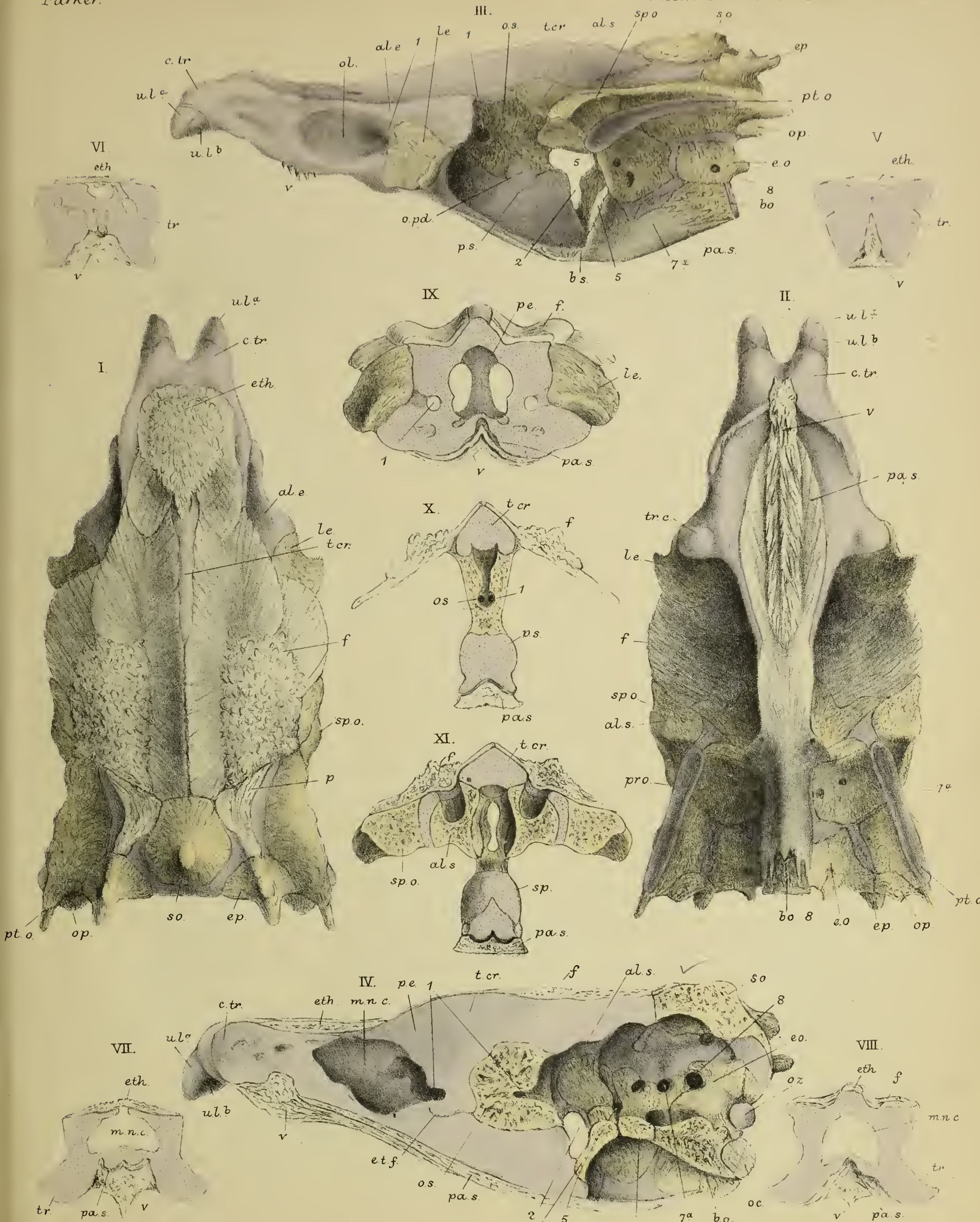
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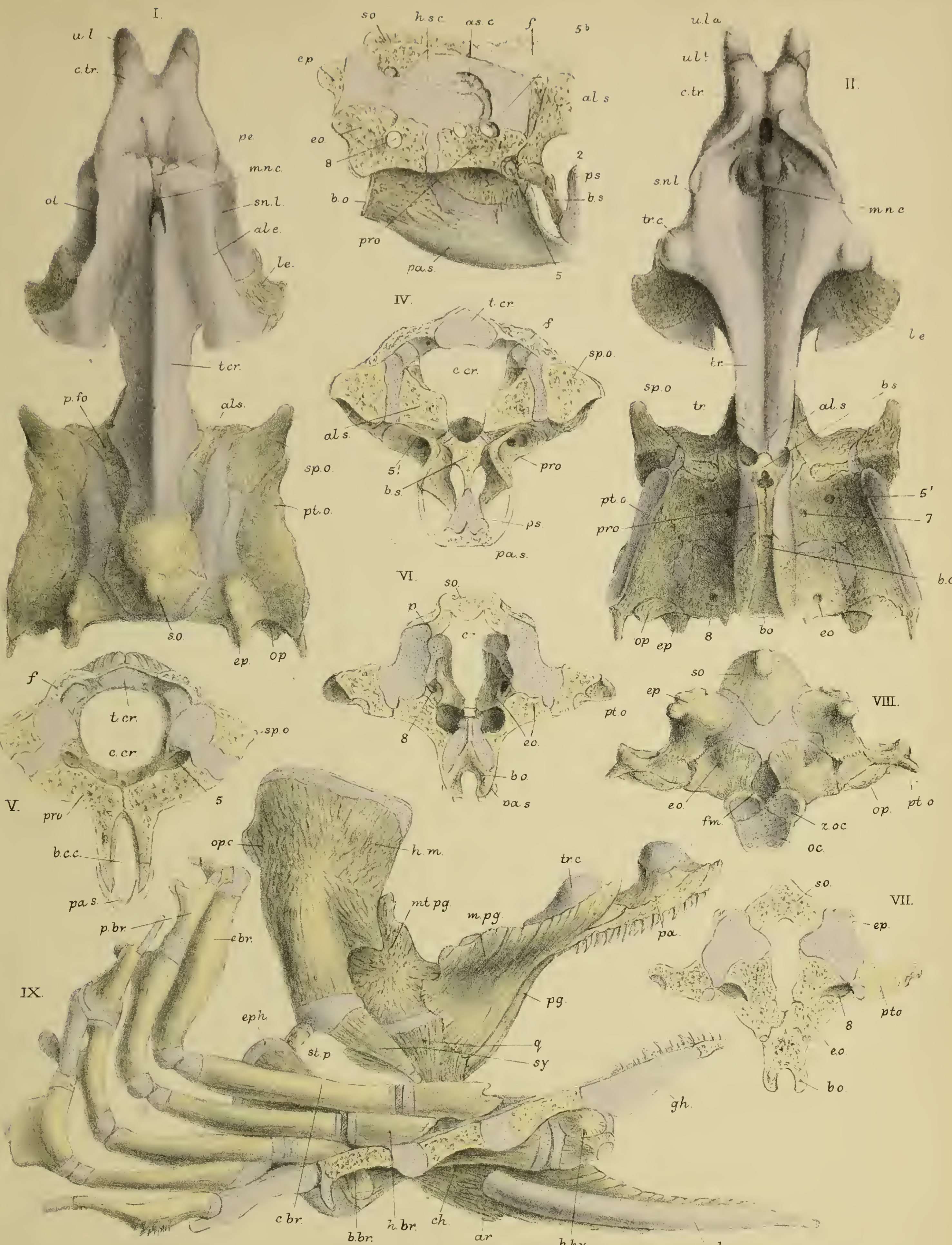
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